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SYMPOSIUM 8

**ECOLOGY AND SOCIAL BEHAVIOUR OF
PARROTS AND PARAKEETS**

Conveners D. A. SAUNDERS and P. C. ARROWOOD

SYMPOSIUM 8

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INTRODUCTORY REMARKS: SYMPOSIUM ON THE ECOLOGY AND SOCIAL BEHAVIOUR OF PARROTS AND PARAKEETS

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The popularity of psittacines as research subjects has never matched their popularity as pets and aviary birds. Because of their longevity and their natural inclination to form close, long-lasting relationships with a mate, they are ideally "preadapted" for human companionship. In addition, their mimetic abilities made many famous as good talkers, endearing them to a public intent on giving them human voices. Unfortunately, these characteristics that have made them so attractive to many people have probably made them seem somehow unreal as birds to scientists. Other factors have also undoubtedly contributed to the paucity of studies on psittacines. For one, psittacines are not usually territorial but range widely and often erratically over a large area. In the tropical forests that many inhabit, their ranging habits make them exceedingly difficult to find and follow, or to catch for banding and marking.

Nevertheless, a few species have been well studied, though primarily in captivity. The Budgerigar *Melopsittacus undulatus*, an Australian parakeet, is probably the best-studied of all psittacines. Studies in the wild by Rothwell & Amadon (1964), Schrader (1975) and Wyndham (1978, 1980a,b,c,d, 1981, 1983) and in captivity by Cinat-Thomson (1926), Masure and Allee (1934), Ficken et al. (1960), Brockway (1962a,b, 1964a,b,c, 1965, 1967a,b,c, 1968, 1969a,b, 1974), Hinde & Putman (1973), Putman & Hinde (1973), Trillmich (1976a,b,c), Stamps et al. (1985, 1987, 1989, 1990), Dooling & Saunders (1975), Dooling & Searcy (1981), Dooling et al. (1987, 1990, in press), Brown et al. (1988), Okanoya & Dooling (in press), and Kavanau (1987) have revealed many fascinating behaviours and abilities. The Australian cockatoos (Carnaby 1948, Pidgeon 1970, 1981, Rogers & McCulloch 1981, Rowley 1980a,b, 1983, 1990, Rowley & Saunders 1980, Saunders 1974a,b, 1977a,b, 1979a,b,c, 1980, 1982, 1983, 1986, 1989, 1990, Saunders & Curry 1990, Saunders & Ingram 1987, Saunders & Smith 1981, Saunders et al. 1982, 1984, 1985, Buckland et al. 1983, Adams et al. 1984, McInnes & Carne 1978, Campbell & Saunders 1976, Schodde et al. 1979, Millam et al. 1988, Myers et al. 1988, 1989, Yamamoto et al. 1989, Joseph 1982a,b,c, Clout 1989, Jones 1987), the Puerto Rican Parrot *Amazona vittata* (Snyder 1977, Snyder & Taapken 1977, Snyder et al. 1987, Wiley 1980), and the Monk Parakeet *Myiopsitta monachus* (Humphrey & Peterson 1978, Caccamise 1980, Bucher & Martin 1987, Martella & Bucher 1984, in press, Martella et al. 1985, 1987, Navarro & Bucher 1990) are the most studied in the wild. Noticeably lacking are studies of most Neotropical (South and Central American), Afro-Asian and Pacific (non-Australian) species. Despite Dilger's (1960, 1962) earlier work with the African *Agapornis* lovebirds, little further scientific interest has been shown in that geographical group of psittacines.

We are very pleased in this symposium to be presenting papers covering Neotropical (Arrowood, Bucher, Gnam) and Pacific (Moorhouse, Saunders) species. With the exception of the Moorhouse study that has just begun, these papers also represent sustained work on a single species for periods up to twenty-two years. Psittacines are generally long-lived birds and many aspects of their ecology and behaviour will not become apparent without such long-term studies, particularly in areas subject to change due to human pressure.

The losses of wild psittacine populations for the pet trade and through habitat destruction will make many species unavailable for study if these destructive trends continue. This will result in more studies like those of the very small population of the Puerto Rican Parrot in last-ditch efforts to forestall extinction. It is our hope that the threat of extinction is not the only stimulus that can awaken more scientific interest in this fascinating group of birds, and we hope that growing popular and scientific concern can save most parrot species from this danger.

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THE EFFECT OF LAND CLEARING ON THE ECOLOGY OF CARNABY'S COCKATOO AND THE INLAND RED-TAILED BLACK COCKATOO IN THE WHEATBELT OF WESTERN AUSTRALIA

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ABSTRACT. European settlement of south-western Australia brought about extensive changes over the last 160 years. Widespread clearing of the semi-arid zone (wheatbelt) for cereal cropping and sheep farming has removed about 93% of the native vegetation, leaving the remainder scattered in small remnants across the landscape. Before these changes, Carnaby's Cockatoo *Calyptorhynchus funereus latirostris* was the only cockatoo occurring throughout this area. It has not been able to adapt to the reduction and fragmentation of its habitat and has disappeared from over a third of its range within the last 20 years. By way of contrast, the Inland Red-tailed Black Cockatoo *C. magnificus samueli* occurred along the watercourses of the arid zone (pastoral area). With clearing for agriculture, this species has expanded its range into the semi-arid agricultural area, invading part of the range of Carnaby's Cockatoo. The Red-tailed Black Cockatoo is slowly expanding its range, moving into areas of heavy infestation of *Emex australis*, an agricultural weed on which it feeds almost exclusively. The biologies of these two black cockatoos are compared in the light of their changing distributions and conservation status.

Keywords: Carnaby's Cockatoo, *Calyptorhynchus funereus latirostris*, Red-tailed Black Cockatoo, *Calyptorhynchus magnificus samueli*, distribution, breeding biology.

INTRODUCTION

The southwest of Western Australia has undergone rapid and extensive change since settlement by Europeans in 1829. In the semi-arid zone (defined here as the area receiving between 300 and 650 mm mean annual rainfall), now known as the wheatbelt (see the unhatched area in Figure 1), an area of 14 million ha has had 93% of the original vegetation removed, over half of it since 1945 (Saunders et al. 1985, Saunders & Hobbs 1989). The remainder is scattered across the landscape in thousands of patches of varying sizes, shapes, vegetation associations, landuse histories and ownership. This change in the distribution and abundance of native vegetation has had major effects on the fauna of the region, the mammals being the first to suffer a wave of extinctions (Kitchener et al. 1980). The avifauna of the wheatbelt is undergoing similar changes, with two species already extinct in the region and many more species changing in distribution and abundance (Saunders 1989; Saunders & Curry 1990).

Before European settlement, only Carnaby's Cockatoo *Calyptorhynchus funereus latirostris* occurred throughout the wheatbelt, with two other species of cockatoo occurring in parts of the wheatbelt; the Long-billed Corella *Cacatua pastinator pastinator* [corella nomenclature follows Schodde et al. (1979)] and Major Mitchell's Cockatoo *C. leadbeateri*. Another three species now occur in the wheatbelt; the Galah *Eolophus roseicapilla*, Little Corella *C. p. gymnopsis* and the Inland Red-tailed Black Cockatoo *Calyptorhynchus magnificus samueli* [Black cockatoo nomenclature follows Adams et

al. (1984)] . Saunders et al. (1985) discuss the way in which clearing native vegetation affected the distribution of all six of these species in southwestern Australia.

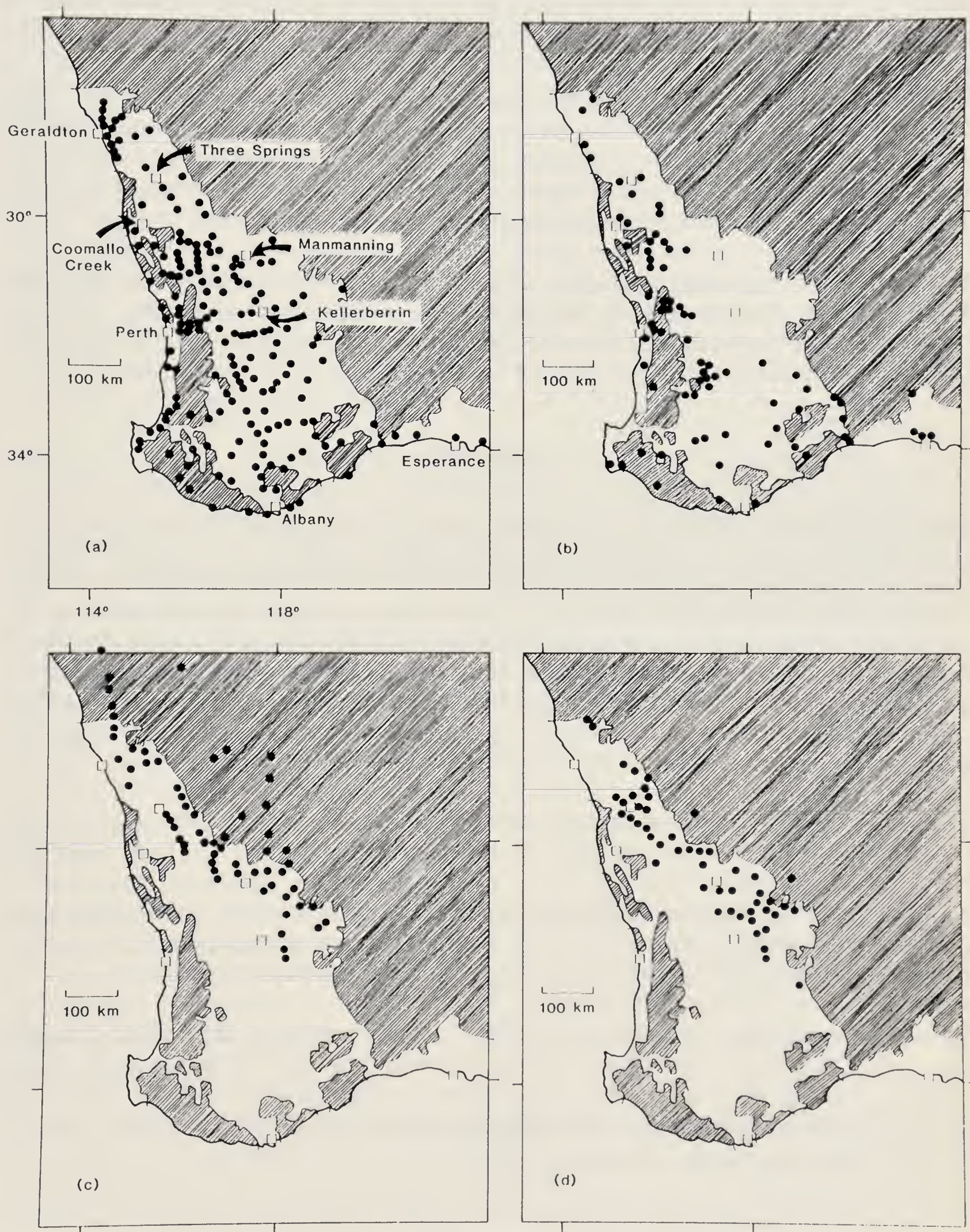


FIGURE 1 – The past and present distributions of Carnaby's and Red-tailed Black Cockatoos. The hatched area represents uncleared native vegetation and the remainder represents cleared land. The wheatbelt is represented by the unhatched area north and east of the line between Perth and Albany. (a) Distribution of Carnaby's Cockatoo in 1968. (b) Carnaby's Cockatoo 1987-89. (c) Red-tailed Black Cockatoo 1961-1965. (d) Red-tailed Black Cockatoo 1987-89.

Carnaby's Cockatoo was the only species that formerly occurred over the entire semi-arid zone; a detailed ecological study of it began in 1969 and is still continuing (Saunders 1979, 1980, 1982, 1986, 1990; Saunders & Ingram 1987). This species nested in hollows in eucalypt trees and fed on seeds and flowers of the Proteaceae which dominated the scrub-heath vegetation.

The Inland Red-tailed Black Cockatoo formerly occurred along the watercourses of the arid zone (defined here as the area receiving less than 300 mm mean annual rainfall), an area further inland from the wheatbelt or semi-arid zone (see hatched area to the north and east of the wheatbelt in Figure 1). It nested in hollows in eucalypt trees and fed on grass seeds and burrs distributed along the river floodplains.

Neither species has taken to feeding on cereal crops, and they have demonstrated entirely different responses to the change in the distribution and abundance of native vegetation. This paper briefly examines these responses and looks at the future of these two species.

METHODS

The distribution of Carnaby's Cockatoo in 1968 is based on the results of a survey conducted through schools throughout the southwest of Western Australia. The distribution of the Red-tailed Black Cockatoo in the southwestern portion of its range between 1961 and 1965 is based on surveys made by Agricultural Protection Board staff. The present distributions of both species are based on weekly observations by residents throughout the wheatbelt who collected data on the avifauna of their areas between May 1987 and December 1989 (Saunders 1989). The distribution of the Red-tailed Black Cockatoo in the arid zone has not been assessed; however, Saunders & Curry (1990) list it as an uncommon nomad of riverine woodland in the arid zone.

The breeding biology of Carnaby's Cockatoo was studied at Coomallo Creek (Figure 1a) between 1969 and the present, and at Manmanning (Figure 1a) from 1969 until 1977, by which time it had become extinct in that area. Methods, described in Saunders (1982), involved the study of individually marked birds, with particular attention to their diet, behaviour, who they mated with, where they nested, the growth of their nestlings, nesting success and movements throughout the year.

The breeding biology of the Red-tailed Black Cockatoo was studied at Three Springs (Figure 1a) between September 1974 and December 1981. The Red-tailed Black Cockatoo has two distinct breeding seasons each year: Autumn and Spring (Saunders 1977); this allowed 14 separate breeding seasons to be studied. Methods were the same as those used with Carnaby's Cockatoo.

RESULTS

Until 1968 Carnaby's Cockatoo occurred throughout the wheatbelt; however, 20 years later it had disappeared from over one third of its previous range and is now absent from the central and eastern wheatbelt (Figures 1a & 1b). In contrast, by the early 1960s, the Red-tailed Black Cockatoo had invaded the northern wheatbelt from the

adjacent arid zone and was moving into the northeastern edge of the central wheatbelt. Thirty years later this species continues its invasion of the central wheatbelt and is slowly extending its range southward (Figures 1c & 1d).

Carnaby's Cockatoo and the Red-tailed Black Cockatoo are approximately the same size [folded left wing 367mm (CC) vs. 379 (RTBC)] and weight (650 g vs. 660 g). The eggs are roughly the same size and weight (32.8 g vs. 33.5 g), representing about 5% of the maternal body weight. Carnaby's Cockatoo normally lays two eggs (clutch size 1.8, N=494), with about eight days between eggs; the second nestling usually dies within 48 hours of hatching. The Red-tailed Black Cockatoo only lays one egg (451 out of 460 clutches). Both incubation periods are about 29 days. The females of both species carry out all the incubation and brooding, being fed by the male during this time. Carnaby's Cockatoo usually fledges only one young, however it may occasionally fledge two young if conditions are favourable (Saunders 1986). The period between hatching and leaving the nest is 77 (SD \pm 4; N=188) days in Carnaby's Cockatoo, regardless of season or breeding area, while the Red-tailed Black Cockatoo takes 84 (\pm 8; N=147) days or 9% longer.

Breeding success, defined as the percentage of nests that produce free-flying young, shows considerable difference between the two species. Carnaby's Cockatoo at Coomallo Creek had an average breeding success of 64.5% (range 58-86%), based on 529 nests over eight years whose history was followed throughout the breeding season. At Manmanning this species had an average breeding success of 35% (range 7-50%), based on 102 nests over 7 years. The Red-tailed Black Cockatoo had a breeding success of only 37.6% (range 24-66%), based on 428 nests in 11 breeding seasons, which represents only 58% of the breeding success of Carnaby's Cockatoo at Coomallo Creek but is similar to that at Manmanning. One hundred and fifty-one (35.3%) nesting attempts by Red-tailed Black Cockatoos failed at the egg stage and 28 (6.5%) of the total nesting attempts failed probably because feral cats climbed the nest tree and preyed upon the nest contents and/or the breeding female. Predation rates by cats varied and in Spring 1978 it reached a maximum of 17.2% of nesting attempts.

In the early 1970s, the breeding population of Carnaby's Cockatoo at Coomallo Creek averaged 69 breeding attempts per year; however, land clearing in the study area led to a reduction of the breeding population which, since 1977, has averaged 43 breeding attempts per season (range 38-52). The Red-tailed Black Cockatoo at Three Springs averaged 25 breeding attempts in Autumn (range 12-38) and nearly twice that at 47 in Spring (range 30-61).

The occurrence of breeding females in the breeding areas, based on the resighting of individually marked birds is shown for a sample of both species in Table 1. Carnaby's Cockatoo bred each Spring and returned to the same area to nest. In many cases they returned to the same hollow, or a hollow near the one used previously. Female UF nested regularly in nest 29 and in 1980 and 1986 she was seen in the study area and was almost certainly nesting somewhere but there was no time available to search for her nest. The other point of interest is that Carnaby's Cockatoos were usually successful in their breeding attempts, renesting if they were unsuccessful early in the season (see UC-1975, US-1976, Table 1).

TABLE 1 – Female occurrence in breeding area, based on the sighting of tagged individuals. A selection has been chosen to illustrate the pattern for each species: (a) Carnaby's Cockatoo; and (b) the Inland Red-tailed Black Cockatoo. * means there was no survey in that period; the number in the year column indicates nest number; + indicates the nesting attempt was successful; - indicates nest failure; **seen** indicates the bird was seen in the breeding area, but no nest was found for that particular period; **ns** indicates the bird was seen that season, but not in the breeding area; **A** = Autumn; **S** = Spring. Female UF was 19+ years old in November 1989.

(a) Carnaby's Cockatoo																
Female	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
UC	64+	65- 53+	53+	53+	*	*	66+	66+	51+	135+	51-					
UD	137+	137+	136+													
UE	148+	178+	178+													
UF	29+	29+	29+	29+	*	*	seen	29+	29+	29+	29+	29+	seen	*	29+	11+?
US	42+	seen	113- 32+	32+	*	*	seen	seen	103+	154+	154+	37+	194+			
(b) Red-tailed Black Cockatoo																
Female	1974S	1975A	1975S	1976A	1976S	1977A	1977S	1978A	1978S	1979A	1979S	1980A	1980S	1981A		
BE		13+	82+		82-											
BG		41+	?-	77-												
PZ			seen	86+	seen	ns	109-									
VB	4+		seen	seen	seen		77-									
SI	14+		11+	ns	ns	ns	seen									
SK	11+		35+	ns	ns	ns	105-									
SP			74+	ns	ns	ns										

The Red-tailed Black Cockatoo demonstrated a different pattern. They rarely used the same hollow to nest in twice and were often unsuccessful. Female BE (Table 1) shows that individual females may nest successfully in both Autumn and Spring (1975). She was not seen in the breeding area the following Autumn, and then returned to breed unsuccessfully in the Spring. Red-tailed Black Cockatoo females that were known to be alive often did not return to the breeding area each season, and when seen outside the breeding area they sometimes had unmarked young with them, indicating they had bred successfully elsewhere. SI was an example of this pattern.

Carnaby's Cockatoo feeds on the seeds and flowers of a wide range of Proteaceous species, particularly the genera *Grevillea*, *Hakea*, *Dryandra* and *Banksia* (Saunders 1980), while the Red-tailed Black Cockatoo feeds almost exclusively on the seeds of an agricultural weed *Emex australis*, an annual and member of the family Polygonaceae. Of 238 observations of Red-tailed Black Cockatoos feeding, 219 (92%) were of feeding on *Emex* and only nine were of feeding on native vegetation (five species). Twenty-one Red-tailed Black Cockatoos examined post-mortem all had *Emex* seeds in the crop and five also had seeds of *Raphanus raphanistrum*, another agricultural weed, in the crop.

DISCUSSION

Comparative studies of the breeding biology of Carnaby's Cockatoo at several locations revealed that the birds' breeding success was markedly lower in areas that had been extensively cleared: the growth rates of nestlings at Manmanning were depressed compared with birds in areas like Coomallo Creek, where extensive areas of native vegetation remained within sight of the nesting grounds. This mosaic of native vegetation over agricultural landscapes, linking remnants to each other, has allowed this species to survive, even though breeding population sizes have decreased (Saunders 1990). The range of Carnaby's Cockatoo will continue to contract as it adjusts to the changes imposed on the landscape by humans. The final result may be as little as half its former range.

The Red-tailed Black Cockatoo is, however, expanding its range into the semi-arid zone adjacent to its historical distribution in the arid zone. In the semi-arid zone, European activities have created a landscape of millions of hectares of riverine plain (Saunders et al. 1985). The Red-tailed Black Cockatoo is gradually invading the areas which have heavy infestations of the agricultural weed *Emex australis* (Gilbey 1974). This plant can be prolific and heavy infestations can provide several million viable seeds to the hectare; furthermore, the seeds may remain viable on, and in, the soil for several years (Gilbey 1974). The Red-tailed Black Cockatoo feeds on this weed almost exclusively and has thus been provided with a constant and plentiful food supply. Nest sites are widely distributed as woodland was left in patches across the landscape. It is not known if the two annual breeding seasons are an adaptation to the semi-arid zone or its native arid zone, as there have been no comparable studies of this species in other parts of its range. The birds are not site specific like Carnaby's Cockatoo. They do remain with conspecifics in feeding flocks and, while breeding, will travel in excess of 40 km per day to join a foraging flock, overflying areas near their nest sites where food is plentiful. The wide fluctuation in numbers of birds breeding in the Three Springs study area each season (12-61) illustrates the

nomadic breeding pattern. This contrasts with the stable population of Carnaby's Cockatoo at Coomallo Creek, which has remained at just over 40 pairs since 1977.

There are several areas of concern in relation to the breeding of the Red-tailed Black Cockatoo in the wheatbelt and these relate to the apparently low breeding success, the high failure rate of eggs and the apparently slow growth rates of the nestlings. Unfortunately there have been no studies of the Red-tailed Black Cockatoo in the arid zone to allow comparisons with the wheatbelt population, so it is necessary to make comparisons with Carnaby's Cockatoo which has been studied in both favourable and unfavourable breeding areas (Saunders 1982). The Red-tailed Black Cockatoo with a breeding success of 37.6% of all nesting attempts is similar to that of Carnaby's Cockatoo (35%) at Manmanning, an area where Carnaby's Cockatoo became extinct. Particularly worrying is that a species which lays only one egg should have a failure rate of eggs of 35.3%. Observations at nests indicated that the females were not consistent in their incubation, readily leaving the nest for long periods, something that Carnaby's Cockatoo did not do, except where food was limiting. In addition, weight increase by Red-tailed Black Cockatoo nestlings was considerably slower than in Carnaby's Cockatoo and demonstrated the same pattern of growth that nestlings of Carnaby's Cockatoo showed in areas where Carnaby's Cockatoo became extinct. These facts seem to indicate that even though the Red-tailed Black Cockatoo is slowly increasing its range, something is affecting breeding success and nestling growth rates. The most obvious cause is the food supply, which is almost exclusively *Emex australis*. It is possible that a diet of *Emex* seeds is not suitable for normal growth of nestlings, however it is hard to see how this would affect the behaviour of the adults and result in elevated failure rate of eggs. *Emex* is often sprayed with a range of herbicides and it is possible that ingestion of these may affect the birds adversely, for example, affecting their behaviour. This possibility has not been tested; however, it is the most likely explanation for the high failure on eggs and the slow growth rates of the nestlings.

With a dependence on one species of weed for food, the position of the Red-tailed Black Cockatoo in the areas it has recently colonised is precarious. Agricultural scientists are working on methods to control and, preferably eradicate *Emex*. If they are successful, that will see the elimination of the Red-tailed Black Cockatoo from the wheatbelt, making the conservation of this species in the arid zone a high priority.

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MALE-MALE, FEMALE-FEMALE AND MALE-FEMALE INTERACTIONS WITHIN CAPTIVE CANARY-WINGED PARAKEET *BROTOGERIS V. VERSICOLURUS* FLOCKS

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ABSTRACT. Psittacine birds are known for their monogamous yet gregarious, flocking nature. Few studies, however, have investigated the nature of inter-individual interactions within psittacine flocks. This paper describes the patterns of interactions within captive Canary-winged Parakeet flocks. Affiliative interactions in these monogamously-paired birds are restricted to the mate and recently-fledged young. Within-pair interactions are egalitarian, with reciprocal allopreening, allofeeding and contact-seeking behaviour. Males and females do not pursue affiliative interactions with nonmates. Both males and females have agonistic encounters, in equal proportions, with the same- and oppositely-sexed nonmate individuals. Canary-winged Parakeets seem different from most birds in the exclusiveness of their monogamy, in the egalitarian nature of their intrapair interactions, and in the equal roles each sex plays in interactions with same- and oppositely-sexed nonmate individuals.

Keywords: Canary-winged Parakeet, *Brotogeris v. versicolurus*, affiliative behaviour, agonistic behaviour, egalitarian behaviour.

INTRODUCTION

The study of social relationships and intra-specific organization in flocking species is still in its infancy. This is in contrast to the large and growing literature on the advantages and disadvantages of the phenomenon of flocking. Because of the far-ranging nature of most psittacine flocks outside the breeding season, studies of their behaviour are difficult. This paper uses captive flocks of Canary-winged Parakeets *Brotogeris v. versicolurus* P.L.S. Muller (nomenclature after Forshaw 1977), a Neotropical parakeet occurring in the wild in flocks of 10-100 individuals (Rocha et al. 1988, Forshaw 1977, Arrowood pers. obs.), to document social relationships, to illustrate what may be some general aspects of psittacine inter-individual behaviour, and, finally, to compare and contrast psittacine social relationships with those documented in other flocking birds.

Psittacine birds are characteristically gregarious (having a positive tendency to join others in a more or less peaceful manner, Moynihan 1958), remaining in groups, if not year-round, then during the nonbreeding portion of the year (Forshaw 1977, Kunkel 1974). Maintenance of an exclusive pair relationship year round also characterizes many psittacines, with evidence of long-enduring pairs in some species (Dilger 1960, Rogers & McCulloch 1981, Serpell 1981, Snyder et al. 1987, Saunders 1982, Arrowood 1988). Furthermore, in many psittacines there is no sexual dimorphism or dichromatism, and no one has documented any intrasexual physical variability that is related to variability in dominance status as in some other flocking birds (Trivers 1985, Rohwer 1977, 1982). For similarly-appearing, paired birds living in flocks, what is the nature of their inter-individual relationships, both within the pair relationship and outside of it?

METHODS

Forty-one individuals and 14 heterosexual pairs of Canary-winged Parakeets were observed in seven different captive flocks (N=1021 individuals/flock) at the University of California, Davis and Irvine, from 1978 through 1988. Some individuals and pairs resided in more than one flock; whenever this occurred, their values from the different flocks were averaged to give a single value for that individual or pair for data analysis.

Unpaired individuals and pairs with differing lengths of pair association resided within the flocks. All subjects for this analysis were at least one year old. Mate changes unrelated to death of a pair member were rare. Whenever flock membership was altered (as in moving birds to a newly-constructed aviary), pairs were kept intact.

Sexual identity of the parakeets was established by surgical laparoscopy, successful breeding, or morphometric measurements (Arrowood, unpubl.). A black dye (Melchior & Iwen 1965) applied to individually-distinct areas of each bird's plumage made the birds instantly identifiable. All parakeets had numbered aluminum leg bands for permanent identification.

The first captive flock was composed of wild-caught, imported birds (Arrowood 1988). Subsequent flocks contained additional wild-caught, imported birds as well as the captive-bred young of flock pairs. I never attempted to tame any of the birds, nor instituted any kind of domestication process with artificial selection for behavioural or morphological traits. All birds were kept in a captive environment behaviourally relevant (Price 1984) to this species, i.e., an environment where their normal flocking behaviour (Arrowood, unpublished data on a wild flock, Shroods 1974) could be and was maintained. Social interactions were not restricted and individuals could freely choose mates.

Housed in large outdoor aviaries (range of 4.6 m wide x 4.6 m long x 2.2 m high to 4 m w x 12 m l x 3 m h), the birds experienced daily and seasonal environmental changes. Successful breeding in all flocks suggests that reproductive and parental behaviour was not detrimentally affected by captivity. Within the aviaries, the parakeets behaved as a flock; movements were often either coordinated or individual/pair movements resulted in the entire group residing in one small part of the aviary. Territoriality did not exist except during the breeding season when pairs became possessive of nest boxes. None of the data for these analyses includes pairs that had eggs or dependent young; thus, reproduction itself did not contribute to inter-individual or inter-sexual relationships (Erickson 1978). A few offspring maintained extended affiliative relationships with their parents; in these analyses, interactions between parents and their independent, but still affiliative, young are not included.

The birds' behaviour was sampled using five-minute focal animal observations (Altmann 1974). All birds were habituated to my presence, so I sat at one site in the open within each aviary. The 41 parakeets included in these analyses were observed on average 7.74 hours each (SD=5.47; range: 1.42 to 24.17 hours).

Affiliative (N=14) and aggressive (N=6) behaviours are listed and defined in Arrowood (1988); this analysis also included “nibble” and “move beside” as affiliative behaviours.

All statistical tests used two-tailed probabilities.

RESULTS

Affiliative Interactions

Affiliative interactions were almost entirely restricted to the mate. Affiliative acts (N=939) by 13 heterosexually-paired males to their female mates averaged 13.9 acts/hr (SE=1.8), compared to 27 acts or 0.13 acts/hr/individual (SE=0.1) to other females (Wilcoxon Matched Pairs Signed-Ranks Test [hereafter WMPSR], T=0, P<0.005). Twenty-two of the 27 acts to nonmate females were by one male who was the object of interest by four females; however, only four of his 22 acts to these females actually involved physical contact (allopreening or allofeeding). The 13 heterosexually-paired males directed only two affiliative acts to other males (0.01 acts/hr/individual; SE=0.01).

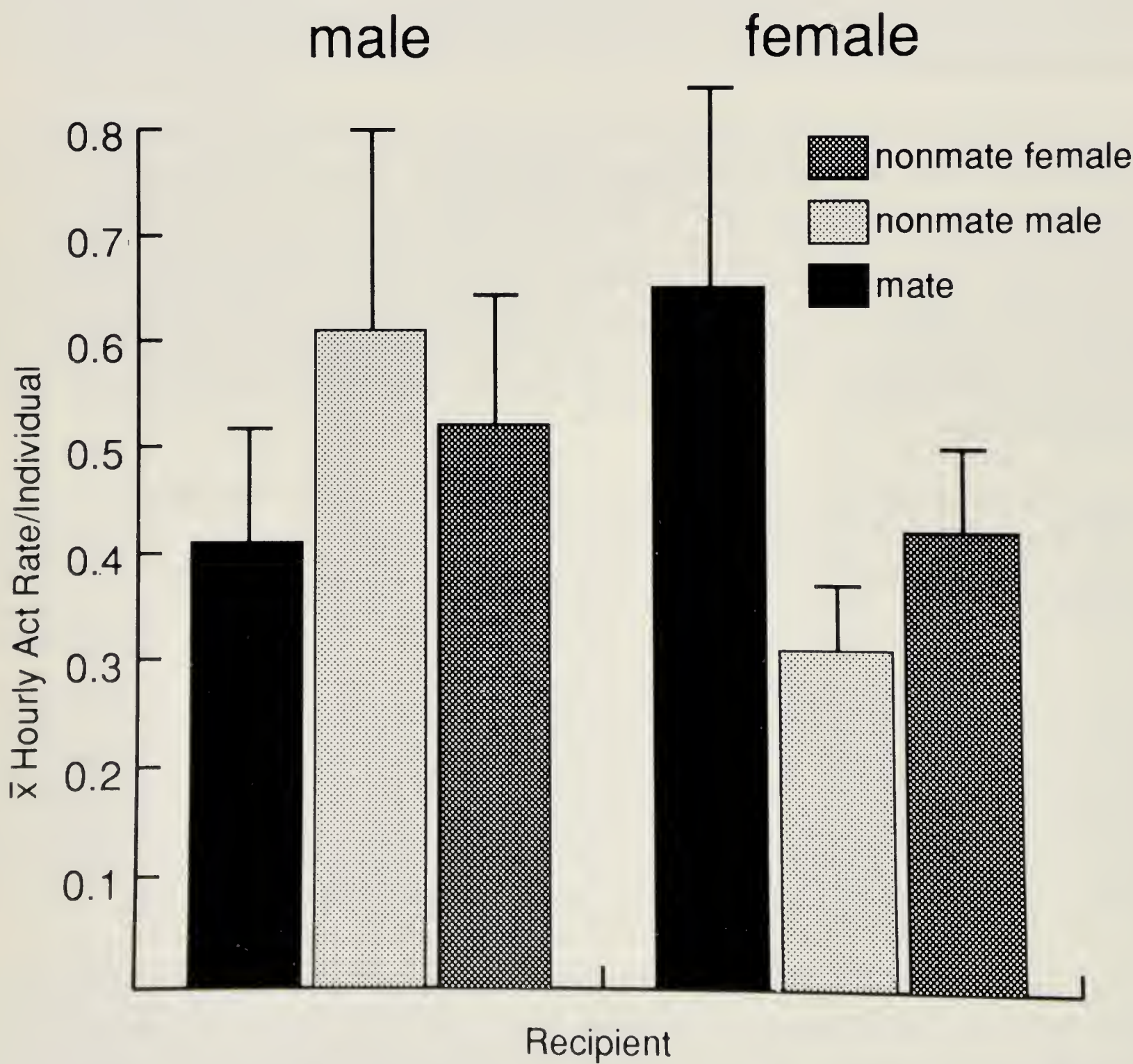


FIGURE 1 – Average hourly rate of aggressive acts by Canary-winged Parakeets against mates and nonmates, \bar{x} (SE). The rate of acts against nonmates is the average hourly rate per individual nonmate.

The 13 heterosexually-paired females similarly restricted their affiliative acts ($N=1285$) to their mates ($\bar{x}=16.9$ acts/hr.; $SE=1.8$) compared to other flock males ($N=3$ acts; $\bar{x}=0.01$ acts/hr/individual; $SE=0.01$) or females ($N=4$ acts; $\bar{x}=0.01$ acts/hr/individual; $SE=0.01$). The difference in the hourly act rate to the male mate vs. other males is highly significant (WMPSR Test, $T=0$, $P<0.005$). All three affiliative acts by females to nonmate males were movements closer to another male. Thus, in contrast to the one paired male who allopreened and allofed nonmate females, no paired females allopreened or allofed birds other than their mates.

Paired females interacted with nonmates of the opposite sex less than paired males did (3 vs. 27 interactions). However, since one male accounted for most of those 27 interactions by males and since most (9 of 13 males; 11 of 13 females) males and females had no affiliative interactions with nonmates of the opposite sex, an analysis of which partner is more likely to initiate affiliative interactions with the opposite sex is not meaningful.

Overall, the Canary-winged Parakeet mates interacted with each other affiliatively at high rates; on average there was one affiliative act within the pair every 2.8 minutes. Although there was a tendency for the female of a pair to direct more affiliative acts to her male mate than vice versa, the difference was not a significant one (WMPSR Test, $T=22.5$, $N=14$, $P>0.05$).

Aggressive Interactions

Canary-winged Parakeets occasionally act aggressively toward their mates (Figure 1). Males directed aggressive acts toward their mates on average about once every two hours ($\bar{x}=0.42$ acts/hr); the rate of aggressive acts by females to their mates was similar ($\bar{x}=0.65$ acts/hr). Out of 14 heterosexual pairs, no aggressive acts were ever observed between partners in three pairs, in one pair the male behaved aggressively toward his mate but she did not reciprocate, and in two pairs there were female to male aggressive acts but no male to female aggressive acts. In the remaining eight pairs there was reciprocal aggression. No significant difference exists between the rate of male aggressive acts to the female mate and female aggressive acts to the male mate (WMPSR Test, $T=17$, $N=8$, $P>0.05$).

In contrast to the lack of affiliative acts to nonmates, aggressive acts against nonmates occurred moderately frequently (Figure 1). For this analysis, males ($N=17$) and females ($N=24$) were used regardless of their pairing status. The rate of male aggressive acts against nonmate females does not differ significantly from the rate of male aggressive acts against other males (WMPSR Test, $T=63$, $N=17$, $P>0.05$). Females, similarly to males, behaved as aggressively against males as they did against females (WMPSR Test, $T=100$, $N=23$, $P>0.05$).

Even though each gender distributes its aggressive acts equally to males and females within a flock, it is still possible for males and females to differ in the frequencies of their aggressive acts to a particular sex. Indeed, comparing the rate of male aggressive acts toward other males with the rate of female aggressive acts toward other (nonmate) males, there is a significant difference (Mann-Whitney U Test, $z=1.932$, $n_1=17$, $n_2=24$, $P<0.0536$), with males having higher rates of aggressive acts to other males. The converse is not true, however: females are not more aggressive to females than males are (Mann-Whitney U Test, $z=0.238$, $P>0.05$).

TABLE 1 – Proportion (%) of nonmate males and females in Canary-winged Parakeet flocks receiving aggressive acts by males and females, \bar{x} (SE).

	% in Flock Receiving Aggressive Acts	
	Males	Females
Aggressor		
Male	44.0 (4.6)	42.1 (6.5)
Female	29.3 (5.1)	34.7 (5.4)

Males and females may also differ in the proportion of others in the flock to whom they direct aggressive acts (Table 1). That is, females might direct aggressive acts to a greater proportion of females than males in a flock. For each of 24 females and 17 males, I determined how many females and males, out of the flock total for each sex, each female or male had directed aggressive acts to. The frequency of acts to an individual was not considered. An average proportion value was calculated for any bird sampled from more than one flock.

The proportion of flock males receiving aggressive acts from females was not different from the proportion of flock females receiving aggressive acts from females (WMPSR Test, $T=156$, $N=23$, $P>0.05$). Similarly, males did not deliver aggressive acts to a greater proportion of flock males than females (WMPSR Test, $T=70$, $N=17$, $P>0.05$). Males, however, did have a tendency to direct aggressive acts to a greater proportion of flock males than females did to flock males (Mann-Whitney U Test, $z=1.707$, $P=0.087$). Males and females did not differ significantly in the proportion of females in a flock to whom they directed aggressive acts (Mann-Whitney U Test, $z=1.27$, $P=0.204$).

DISCUSSION

Among monogamous species in which the members of a pair stay together continuously (see Oring 1982), there may be few other groups in which affiliative interactions between partners occur at as high levels year round as they do in psittacines (but see Zann 1977). Since Canary-winged Parakeets have no courtship displays (Arrowood 1988), this record of frequent affiliative interactions is even more impressive. The benefits of frequent interaction within established pairs have not been tested. Arrowood (1988) found that among newly-established pairs, intrapair affiliative interactions were not high at the beginning of pairing; thus, frequent affiliative interactions did not seem to be required for the establishment of a pair relationship. In monogamous grassfinches *Poephila*, birds that formed pair bonds did not differ in the type or frequency of inter-individual interactions from birds that did not form bonds, but the most rapidly-formed pairs had reciprocally-directed interactions of the same degree (Zann 1977).

Enduring season-to-season pairing may be reproductively efficient (Kunkel 1974), with continual affiliative interactions maintaining familiarity between partners, and, thus, making courtship displays unnecessary and/or enhancing behavioural and hormonal synchrony (Erickson 1978). Some captive parakeet pairs do seem to breed more “ef-

ficiently" than others, but the data are insufficient to determine if differing levels of breeding efficiency are correlated with intrapair affiliative interactions. Alternatively, the advantages to perennial monogamy might accrue outside the reproductive season (Oring 1982), selecting, possibly, for increased affiliative interactions during non-reproductive periods compared to the breeding season.

Frequent affiliative interactions, on the other hand, may be a mate-guarding strategy; proximity to the mate and behaviours that occupy the mate's time might prevent both the mate's gallivanting and incursions by others on the mate. Canary-winged Parakeet males, however, have shown no evidence of gallivanting, even though some females have pursued pairing opportunities with them. Adult females, on the other hand, seem to be the ones to leave established pair relationships to pursue pairings (not just copulations) with other males; even so, these cases have been rare in the captive flocks (Hammond, Yamamoto & Arrowood, unpubl.).

In monogamous Bewick's Swans *Cygnus columbianus bewickii*, Scott (1980) found that partners benefitted from continual spatial proximity; females that remained close to their mates spent more time feeding, were threatened less frequently and were more successful in aggressive interactions than when some distance from their mates. Separated males experienced less severe effects, but alone they were less successful in aggressive encounters and were threatened more by others. No data were given on intrapair interactions. And in Cockatiels *Nymphicus hollandicus*, Yamamoto et al. (1989) found that birds force paired at the onset of environmental conditions stimulatory to breeding had lower reproductive activity scores than other groups where partners had greater opportunities to exchange social interactions and thus enhance mate familiarity prior to breeding.

Aggressive interactions in Canary-winged Parakeets were distributed in an egalitarian fashion (Hand 1986) to males and females in the flock. Even though parakeet partners sometimes acted together in directing aggressive acts to others, alone they were just as likely to act intersexually as intrasexually. The only significant trend was for males to direct more frequent aggressive acts to males than females did to males. Psittacines may again be unique in that males and females have equal roles in intraflock aggression.

Given the psittacine flock organization as a grouping of persistent pairs, our notions of male-male aggression, female subordination to males, and male-female courtship, based mainly on temperate territorial species, may have to be modified. Even compared to other flocking species, psittacines may show many differences.

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NESTING BEHAVIOUR OF THE BAHAMA PARROT *AMAZONA LEUCOCEPHALA BAHAMENSIS* ON ABACO ISLAND, BAHAMAS

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ABSTRACT. Although the Bahama Parrot was once abundant and ranged throughout the Bahamas archipelago, it is endangered now and survives only on two islands- Abaco and Great Inagua. Bahama Parrots on Abaco nest in limestone solution cavities beneath the ground, a habit unique among New World psittacines. Between 1985 - 1988, I located and monitored 76 parrot nests in two nesting areas on southern Abaco. Eggs were laid in late May and early June and hatched asynchronously, 26-28 days after the female began incubation. While the female incubated the eggs, the male visited the nest on average four times per day to feed her. After the first week post-hatching, the female left the nest to forage with the male. Parents returned to their nests four to six times per day to feed the nestlings. Chicks fledged asynchronously in late August and early September, 56-58 days after hatching. Bahama Parrots exhibited low reproductive success; successfully nesting pairs fledged a mean of 1.79 ± 0.16 chicks per nesting effort.

Keywords: Bahama Parrot, *Amazona leucocephala bahamensis*, Abaco Island, nesting behaviour, parental care, subterranean nesting.

INTRODUCTION

The Cuban Parrot *Amazona leucocephala* is a polytypic species with five recognized subspecies: *leucocephala* (Cuba), *palmarum* (Western Cuba and Isla de la Juventud), *caymanensis* (Grand Cayman), *hesterna* (Cayman Brac) and *bahamensis* (Bahamas) (Bond 1956). Although the Bahama Parrot was probably present on all major islands in the Bahama archipelago, historically it was recorded from Abaco, New Providence, San Salvador, Long Island, Crooked Island, Acklins and Great Inagua. Today, this species is listed as endangered and persists only on the islands of Abaco and Great Inagua. In recent years, the Abaco population has declined as a result of habitat destruction, logging activities, development, Hurricane Betsy in 1965, and hunting pressures (Attrill 1981, Snyder et al. 1982).

Bahama Parrots were studied by Snyder et al. (1982), who estimated the Abaco population to number less than 1000 birds. Current population estimates range from 860 to 1300 parrots (Gnam 1991). Unlike the Inagua population and other subspecies of *leucocephala* which nest in tree cavities, parrots on Abaco nest in limestone solution cavities beneath the ground, a habit unique among New World parrots (Forshaw 1989).

The Abaco population of the Bahama Parrot is found in Caribbean pine *Pinus caribaea* and mixed broadleaf coppice (native, evergreen hardwood) areas of southern Abaco.

As part of a larger investigation into the breeding biology of *bahamensis*, I studied the nesting behaviour of the Abaco population. With the notable exception of studies on

the Puerto Rican Parrot *Amazona vittata* (Snyder et al. 1987), the Kakapo *Strigops habroptilus* (Merton et al. 1984) and Australian psittacines (Rowley 1980, Wyndham 1981, Saunders 1982), data on the nesting behaviour of parrots in the wild are often anecdotal, fragmentary and based on the observations of one or two nesting pairs. The objectives of my study were to (1) investigate the behaviour of the Bahama Parrot throughout the stages of its nesting cycle, (2) determine the pattern of parental care, and (3) compare its nesting behaviour with other Caribbean *Amazona*.

STUDY AREA AND METHODS

I studied Bahama Parrots in an area 64 km south of Marsh Harbour (Latitude 26° N, longitude 78° W), Abaco Island, from early May to September each year, 1985 through 1988. Since 1985, I located 76 nests but not all of these nests were active in a given year. Clutch size was recorded in all active nests and nests were checked at least once a week until chicks fledged or the nest failed. Observation blinds were placed 10-15 m from the nests of five pairs and the behaviour of these pairs was recorded from sunrise to sunset (a 14-15 hour period). These nesting pairs were observed at least once a week from egg-laying until chicks fledged or the nest failed.

Due to risks associated with tagging parrots (Saunders 1988), I did not try to capture and tag individuals, but instead recognized them by the usually considerable differences in their plumage markings and other physical characteristics. These physical differences were consistent through a season and from year to year. Initially, the five nesting pairs to be observed were selected randomly from a pool of active parrot nests but in succeeding years, pairs which returned to the same nest cavity were given observational preference over newly found nests.

The external and internal dimensions of nest cavities were measured to the nearest 0.5 cm. Nest depth was measured from the lip of the nest to the floor of the nest cavity.

I used the SAS (1985) software package on an IBM mainframe system (at the City University of New York) for statistical analyses.

Data were pooled over the four years of study and provide a general view of nesting behaviour in this unique population. Unless otherwise specified, mean values with their standard errors are reported.

RESULTS

Bahama Parrots on Abaco are monogamous and seasonally defend their nest site. Mates remain together throughout the nesting cycle to produce a single brood.

Nest site characteristics

Although Carraway and Carraway (1979) reported a Bahama Parrot nest on Abaco in the hollow of a Pond Top Palm *Sabal palmetto* and I searched for nests in this area, all of the nests which I located were in limestone-solution cavities beneath the ground, the normal pattern for this population. Nest cavity entrances measured on average

18.3 ± 0.9 (S.E.) cm vertically and 19.8 ± 1.0 cm horizontally. Nest cavities were more spacious internally and on average measured 39.9 ± 2.4 cm by 27.9 ± 1.1 cm. The mean nest depth (N=70) was 125.1 ± 6.6 cm; 74.3 percent of these nests ranged from 51 - 150 cm in depth. Nine percent of the nests had two entrances and 74% (N=52) of the nest cavities had internal ledges or rocky overhangs within them to protect and conceal the eggs.

Incubation

Clutches of 2 - 6 eggs (mean 3.6 ± 0.2) were laid in late May or early June. The frequency of 2-egg nests was 4, 3-egg nests was 19, 4-egg nests was 31, 5-egg nests was two and 6-egg nests was one. Egg-laying was asynchronous and eggs were generally laid at two day intervals. Eggs were incubated exclusively by the female. Most females began incubation with the laying of the first egg. Incubation may have been irregular until the clutch was completed. The incubation period was 26 - 28 days. Incubating females never left their nests except to be fed by their mates. There was no relationship (polynomial regression, $P > 0.05$) between the time that a female spent off the nest and the stage of incubation. Females spent an average of 62.1 ± 3.9 minutes per day off the nest.

Males spent little time in the nest area except when feeding their mates. When males arrived in the nest area, they perched in a nearby pine or shrub and called to their mates. Females exited the nest on average 11.5 ± 1.4 minutes after the male arrived to feed them. Females recognized and responded to the calls of their own mates and never left their nests when neighbouring males called. During incubation the male on average fed the female four times per day with food transfers (N=170) lasting an average of 16.0 ± 0.9 minutes for the various pairs. Most feedings occurred in the morning and late evening. Generally, males fed the female in nearby pines in the nest area. A female was fed in the nest only if she remained in the nest after repeated, unsuccessful male visits and calling. During egg-laying, copulation often followed food transfers. Copulatory behaviour followed the pattern described for other *Amazona* species (Skeate 1984, Snyder et al. 1987). The male perched beside the female with one foot and rested his other foot on his mate's back while she swayed her tail back and forth horizontally against his tail, making cloacal contact.

Pairs gave loud, territorial high-squawk calls when they returned to the nest. Females then immediately entered the nest and resumed incubation. Males flew off to forage and roost, often accompanied by neighboring males. Males did not roost in the nest or nest area in the evening. They roosted communally in large flocks (50-60 parrots). Two roost sites were located 300 m and 1000 m from the main nesting area.

Nestling Period

Eggs hatched asynchronously in late June and early July. The pattern of female care remained unchanged from that which was seen during incubation until about a week after hatching (Figure 1). At this time females started to forage with the males, spending more time off the nest but returning to feed and brood the chicks. There was no apparent relationship between brood size and the amount of time the female spent off the nest (ANOVA, $P = 0.63$) (Figure 1). As the chicks grew older, the time that the female spent off the nest increased until she foraged consistently with her mate during the day and returned to the nest only to feed the chicks (Figure 1). By the fourth week post-hatching, most females no longer roosted in the nest; at this stage, the chicks' body feathers had erupted from the shafts, particularly on the back, wings and thighs.

Males continued to feed the females directly the first week post-hatching and rarely entered the nest to feed the chicks (Table 1). As females decreased daytime brooding of the chicks, males gradually increasingly entered the nest and fed the chicks directly (Table 1). In contrast to the female's barely observable, secretive entry into a nest, the male's initial entries were awkward and took longer. Males lingered on the nest lip, obviously uneasy at entering.

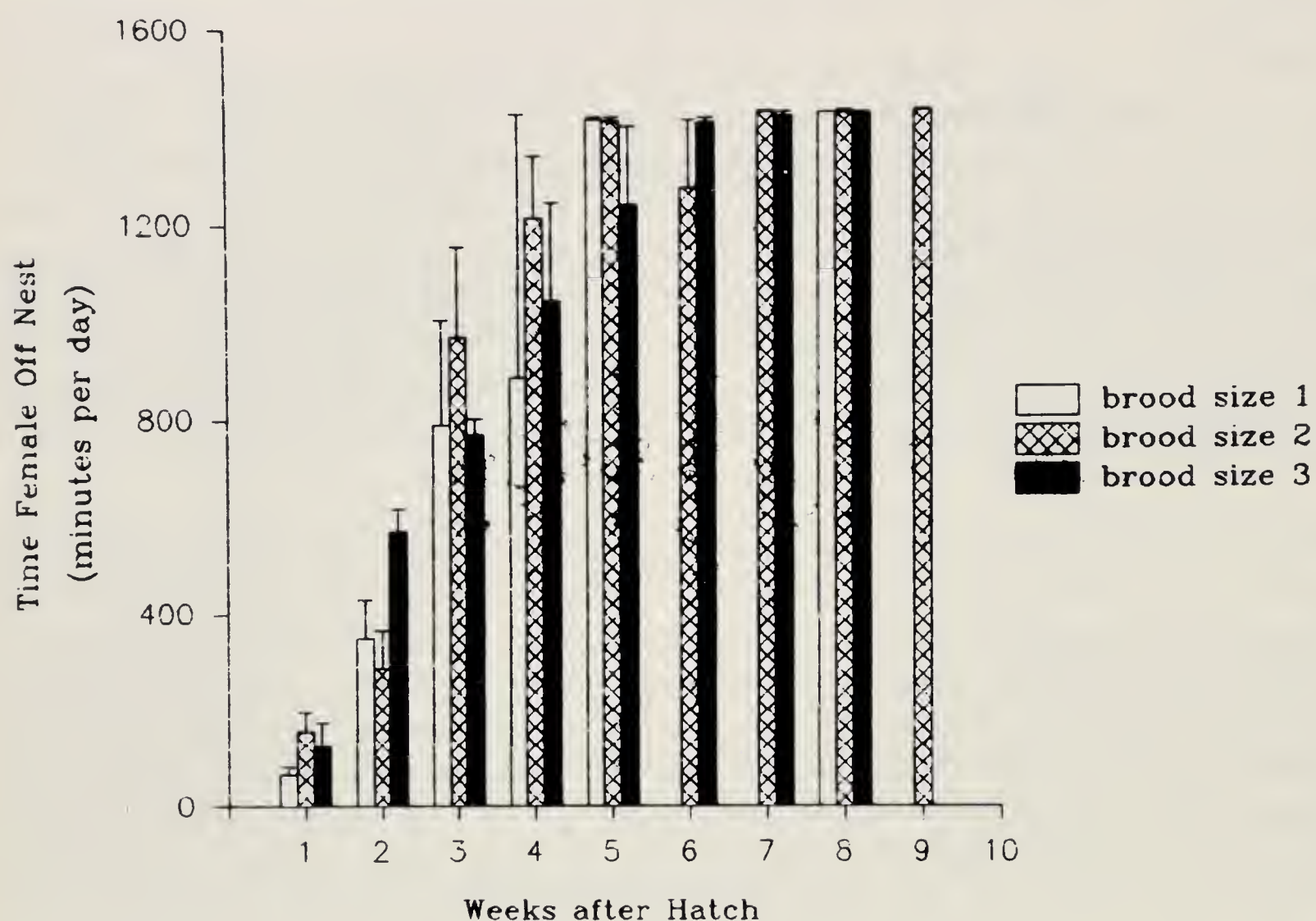


FIGURE 1 – Time spent off the nest as a function of brood size for female Bahama Parrots *Amazona leucocephala bahamensis* on Abaco Island, Bahamas, 1985-1988. Values shown are means with their standard errors. Samples sizes (N) for brood size one were 4,8,4,2,4,1; for brood size two : 6,8,5,7,2,5,5,3,3 and for brood size three : 5,4,4,4,4,4,4,4.

Once females no longer roosted in the nest, males and females returned together to the nest four to six times per day to feed their chicks. Males and females showed no differences (ANOVA, $P=0.53$) in the amount of time that they spent in the nest after the female ceased overnight roosting (Figure 2). Visit time decreased for both males and females at the same rate (ANOVA, $P=0.44$) as fledging approached (Figure 2).

Fledging

Chicks fledged asynchronously (usually 24-48 hours apart) in late August and early September, 56-60 days after hatching. Several days before fledging, chicks began to appear at the nest lip when their parents were in the nest area. The chicks' initial appearances were brief (less than two minutes) but gradually, more of the chick's body protruded from the nest cavity until the chick fledged. As fledging approached (eight weeks post-hatching), parents spent little time inside the nest and despite the chicks' vigorous begging, feedings were brief (Figure 2, Table 1). From a tree or a shrub within 3 m of a nest, parents called to the chicks, apparently coaxing them from

TABLE 1 – Nest attendance by male Bahama Parrots *Amazona leucocephala bahamensis* on Abaco Island, Bahamas, 1985-1988.

Nestling period (week)*	Males (N)	Daily nest visits		Total time spent in nest (minutes per day)	
		Mean	SE	Mean	SE
1	15	0.5	0.2	5.4	2.6
2	20	1.5	0.4	16.7	4.7
3	14	2.6	0.5	20.4	4.9
4	14	4.1	0.2	29.0	3.2
5	12	4.9	0.3	32.3	4.1
6	11	5.5	0.6	28.9	4.2
7	10	4.2	0.6	19.1	4.1
8	10	3.6	0.5	12.4	2.8
9	3	1.7	0.7	4.3	1.9

* Day first chick hatched counted as day 1.

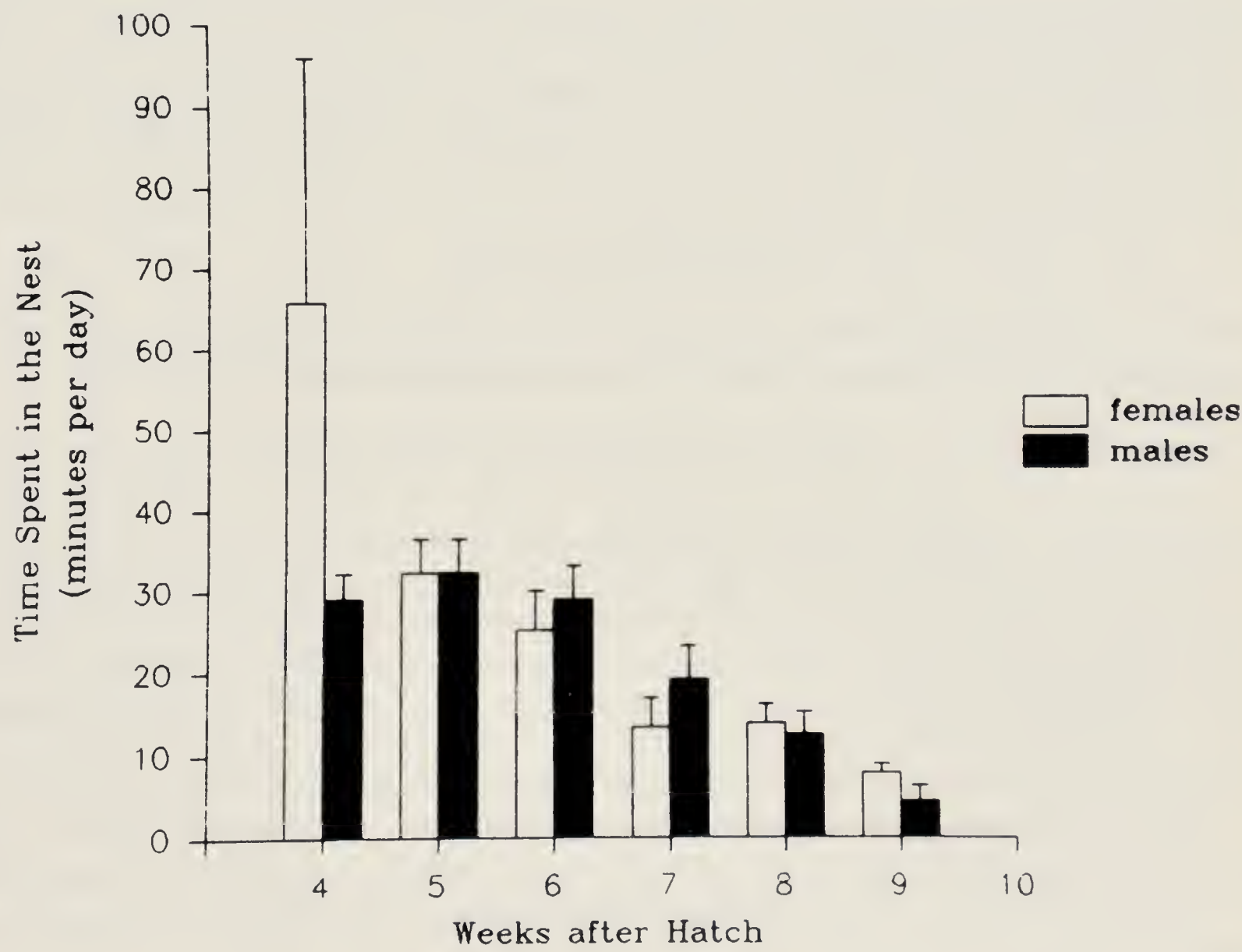


FIGURE 2 – Total time spent in the nest by male and female Bahama Parrots *Amazona leucocephala bahamensis* on Abaco Island, Bahamas, 1985-1988. Values shown are means with their standard errors. Sample sizes (N) for males and females were 14, 12, 11, 10, 10, 3.

the nest. I observed nine fledgings; 67% occurred in the morning and always when the parents were present. Upon fledging, chicks flew considerable distances (> 300

m) accompanied by their parents; chicks had left the nest area by sunset. All fledging flights observed were silent and, except for begging during food transfers, the young and their parents remained virtually silent in the days following fledging.

Nesting Success

An extensive analysis of nesting success data is presented in Gnam (1991), but a brief review of these results follows here. During the years 1985-1988, the mean clutch size at hatching was 3.5 ± 0.1 but the mean number of parrot chicks hatched per nest was 1.88 ± 0.1 . Forty-six percent of all egg-laying pairs fledged young. Successful pairs which hatched at least one chick, fledged a mean of 1.79 ± 0.16 chicks. Causes of nest failure were (in descending order of importance): predation by feral cats *Felis catus*, land crabs *Cardisoma guanhumi*, snakes, and rats *Rattus rattus*; chick deaths from unknown causes; abandoned eggs; flooding of nest cavities; and human disturbance (poaching of chicks).

DISCUSSION

The general pattern of nesting behaviour in Bahama Parrots follows that seen in other species of *Amazona* (Snyder et al. 1987, Silva 1989). Some exceptions to this pattern are noteworthy and likely related to this species' ecology. Although egg-laying in most Caribbean *Amazona* species occurs in late winter or early spring (Feb. - Mar.) (Snyder et al. 1987), the Abaco population of the Bahama Parrot lays its eggs in late spring. Its late breeding season coincides with the peak abundance and availability of its food sources during nesting (Gnam 1991). Caribbean pine produces immature(unripe) pine cones during June through August and poisonwood *Metopium toxiferum* and wild guava *Tetrazygia bicolor* fruit at this time. These food items accounted for 74% of the observed diet during the nesting period (Gnam 1991).

Although the incubation pattern of Puerto Rican and Bahama Parrot females is similar (females spend less than 100 minutes per day off the nest to be fed by their mates), the female patterns differ once nestlings appear (Snyder et al. 1987). During the fourth week post-hatching, female Bahama Parrots no longer roost in the nest in the evening, unlike female Puerto Rican Parrots which roost in the nest until chicks fledge. White-tailed Black Cockatoo *Calyptorhynchus funereus* females cease roosting in the nest about 2-3 weeks before chicks fledge (Saunders 1982). In the Bahama Parrot, roosting in the nest with chicks may be related to the feather and thermoregulatory development of the chicks, rather than to nest defense from predation. Abaco has been devoid of mammalian predators until the relatively recent introduction of cats and rats by man. On at least two occasions, I observed a female who had ceased overnight nest roosting return to her nest and brood chicks during a heavy rainfall.

In the Puerto Rican Parrot, females with larger sized broods reach a plateau of time off the nest earlier in the nestling period than do females with small broods (Snyder et al. 1987). Brood size seems not to affect the time that female Bahama Parrots spend off the nest. My sample size may be too small to detect differences; alternatively, presently unknown ecological factors may be responsible. Subterranean nesting may provide a more stable thermal environment, so that females with even small-sized broods can safely leave chicks. Food sources may be limiting, patchily distrib-

uted and/or require considerable handling time and therefore, regardless of brood size, females must forage after the first week post-hatching to feed themselves and their chick(s).

The parental care pattern of Bahama Parrots in which females are responsible for the incubation of eggs and brooding of nestlings and both sexes feed the nestlings, is similar to that seen in large psittacines, such as the Puerto Rican Parrot (Snyder et al. 1987) and White-tailed Black Cockatoo (Saunders 1982). Although male and female Bahama Parrots visited the nest together to feed the chicks and spent comparable amounts of time in the nest, they may still differ in their interactions with the nestlings. We could not observe behaviour within a nest. In large broods, parents may feed the chicks differentially as do parakeets (Arrowood & Flint in press).

Despite considerable parental care and time expenditure, Bahama Parrots fledge few offspring and reproductive success is low when compared with other Caribbean *Amazona* species (Gnam 1991). Eighty-two percent of all egg-laying Hispaniolan Parrots *Amazona ventralis* fledge 2.5 chicks while 69% of all egg-laying Puerto Rican Parrots fledge 1.8 chicks (Snyder et al. 1987). Various factors affect the reproductive potential and output of this island species (Gnam 1991); but its ground-nesting habit has put the species at risk from nest predation by introduced mammals. Nesting behaviour patterns which were selected for in stable environments may be disadvantageous in a rapidly changing environment.

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SOCIAL BEHAVIOUR AND POPULATION DYNAMICS OF THE MONK PARAKEET

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ABSTRACT. A marked population of Monk Parakeets *Myiopsitta monachus* was studied for eight years in two localities in Córdoba, Argentina. We made observations on behaviour and measured population density, natality, mortality, emigration and immigration. Monk Parakeets are resident year-round, with limited movements during winter. They nest solitarily or in colonies. The Monk Parakeet is unique among parrots in that it builds large enclosed stick nests, which are often integrated in a compound nest that may include several isolated chambers. Parakeets continue to roost within their nests throughout the whole year. Single nests often develop into large compound nests in which different breeding pairs occupy separate nesting chambers. Members of a compound nest may also include nonbreeding individuals occupying separate chambers. These parakeets do not defend an all-purpose territory, defense being restricted to the nests. Juveniles continue to roost in the parental nest during autumn and winter but leave permanently before the following breeding season. Dispersal distance from birth to breeding place is reduced, averaging 1.2 km. We observed a few cases of allofeeding; helping in nest building, maintenance, and vigilance were observed in all birds occupying a compound nest. Breeding was delayed until at least two years of age. Annual survival of first year birds was estimated to be 61%, whereas adult survival was 81%. Our results suggest that the Monk Parakeet's breeding system and population dynamics show several characteristics of a communal breeder, a breeding system not previously recorded in parrots.

Keywords: Monk Parakeet, parrots, Chaco, Argentina, population dynamics, communal breeding, birds as agricultural pests.

INTRODUCTION

The Monk Parakeet *Myiopsitta monachus* occurs in Argentina, Bolivia, Brazil, and Uruguay, where it is considered an agricultural pest (Bucher & Bedano 1976). It is also trapped for the pet trade, around 19,000 birds being imported annually into the USA alone (Nilsson 1990). Despite intensive killing from control campaigns and trapping, the bird is still abundant throughout its range. Moreover, it has become established in other countries where it escaped or was released accidentally, including Puerto Rico and the continental USA (Bull 1973, Neidermyer & Hickey 1977).

The species is unique among parrots in that it builds its own nest of sticks. Nests are often integrated into a compound nest that may include several isolated chambers, each one occupied by a different pair (Forshaw 1978), resembling those of the Sociable Weaver *Philetairus socius* of Africa (Collias & Collias 1977). As indicated by Brown (1987), compound nests or lodges have been traditionally omitted from most discussions of avian helping and communal breeding systems but nevertheless deserve attention given that collaboration in nest building represents an important form of helping (see below).

Intraspecific helping has been found in the Sociable Weaver (Collias & Collias 1977), but not in wild populations of the Monk Parakeet, although S. Emlen (in press) noticed the existence of helpers in captive colonies.

In this report we provide a broad outline of the basic features of the social organization, breeding biology, and population dynamics of the Monk Parakeet. We discuss the possible existence of communal breeding behaviour as well as the adaptive forces that may have favoured its evolutionary development in the Monk Parakeet.

METHODS

Research was conducted from 1982 to 1989 in two different study sites in the province of Córdoba, Argentina. The first is located at San Antonio Ranch ($31^{\circ} 25'S$, $62^{\circ} 59'W$), 8 km east of the town of Arroyito; the second at Los Leones Ranch ($31^{\circ} 05'S$, $64^{\circ} 11' W$), 10 km south of Jesus Maria city. Both areas are under a semi-arid climate regime, rainfall being 870 mm at Jesus Maria and 700 mm at Arroyito. The rainfall pattern is very seasonal, with around 80% of the precipitation concentrated during summer (October-March). The original landscape was parkland with patches of xerophytic woodland, which has been largely cleared for agriculture and cattle-raising.

Observations on general behaviour were made at San Antonio Ranch from an observation tower located near nests on both native and introduced trees (mostly *Eucalyptus* trees). Birds were trapped from the nests at night using a large net able to embrace an entire compound nest (Martella et al. 1987). The parakeets were kept in small cages during the rest of the night, marked with aluminium rings the following morning and then released. We used anodized colour aluminium rings to identify individual birds from a distance, but it proved to be extremely difficult because the Parakeet's legs are very short and covered with feathers. Coloured plastic rings or wing tags also proved unusable because they were rapidly destroyed by the birds, which usually resulted in serious self-inflicted injuries. Some of the birds were also dyed with Rodamine B to help long distance identification.

Population dynamics studies were carried out at Los Leones Ranch from 1983 to 1989 in a study area of 604 ha of native vegetation. Total population counts were obtained through trapping birds from the nests at night in March (post-reproductive season), June (winter), and September (pre-reproductive season), complemented with direct observations during daytime. All captured birds were banded with numbered aluminium rings. Recapture of banded birds from the study area and from within a 200 m wide strip surrounding the study area allowed us to estimate survival, emigration, and immigration.

During the breeding season all nests below a height of 6 m (the upper limit of our accessibility via a portable ladder) were inspected every 10 days on average, and nestlings were banded with numbered rings at about 20 days old. These observations provided data on productivity, reproductive success, and dispersal. We were unable to differentiate sexes from external characteristics, neither could we age adult birds. However, fledglings could be distinguished from adults with reasonable accuracy during the first three months of life because they do not undergo an autumn moult (Navarro et al. unpublished data).

RESULTS

Habitat requirements

The Monk Parakeet inhabits semi-arid savanna woodlands and thickets with xerophytic vegetation, particularly the Chaco scrub and woodland, where it prefers open areas with scattered trees. Availability of tall trees or poles is essential for nesting. Monk Parakeets prefer to locate their nests on the highest available perches, from 3 m to 25 m or more in *Eucalyptus* trees. Lack of nesting habitat may be limiting, at least in some areas within the parrot's range, as shown by the Monk Parakeets' tendency to expand into areas with low vegetation whenever introduced tall trees or electricity poles become available (Bucher & Martin 1987). Consistent with this tendency, the species has expanded considerably and become abundant in agricultural areas of the open Pampas of Argentina, Uruguay and Brazil, following the widespread introduction of *Eucalyptus* trees (Forshaw 1978, Ridgely 1980, Bucher & Martin unpubl. data).

Food and foraging

Monk parakeets feed both in trees and on the ground. Seeds are the staple food, particularly from small grasses (Bucher et al. unpubl. report) Thistles are very important during the breeding season. The birds also eat fruits and flowers, as well as animal food in some cases (mostly insect larvae) (Forshaw 1978, Bucher et al. unpubl. data). Monk Parakeets also feed on grain crops (particularly corn, sunflower, and sorghum) as well as cultivated fruit trees like peaches and pears (Bucher & Bedano 1976).

Social system

SPACING AND FEEDING BEHAVIOUR. Monk Parakeets may nest solitarily or in colonies. Colonies include single compound nests, in which within one large structure each pair has its own chamber with an entrance tunnel, or an aggregation of single and compound nests usually on a single tree or on a few closely-located trees. The parakeets do not defend an all-purpose territory, territorial defense being restricted to the nest colonies. Monk Parakeets feed in flocks of up to several hundred individuals in winter, flocks being restricted to one to four individuals during the breeding season. Feeding areas change throughout the year. During the non-breeding season, the birds stay in the general feeding area, roosting in any nests available in the area. In these situations up to three or four individuals may roost in each chamber (Martin & Bucher unpubl. data).

THE BASIC SOCIAL UNIT. The basic reproductive unit is a breeding pair occupying a nesting chamber, either in a solitary nest or in a compound nest. However, members of a compound nest or a nesting colony may include non-breeding individuals occupying separate chambers (usually in pairs or trios). All members of a compound nest, including non-breeding adults and yearlings, participate in bringing material to the nest and building and maintenance activities (Martella & Bucher in press).

Social interactions among group members are varied and occur constantly throughout the day. The species is very noisy, with calls uttered almost constantly. At least 9 different calls have been identified that elicited specific responses from other individuals when played back (Martella & Bucher 1990).

BREEDING BEHAVIOUR. Nests are made with thorny twigs. Monk Parakeets spend an impressive amount of time and energy in carrying and manipulating material for nest building and maintenance. Nest building and maintenance is particularly intense in spring before the start of the breeding season and in early autumn (Figure 1) (Martella & Bucher in press). Compound nests originate and grow as other birds build their nests attached to existing chambers. Sometimes newcomers have to overcome strong aggressive challenges from the original nest's occupants. Providing that adequate support is available, nests may grow to enormous proportions. For example, a geodesic tower in Cordoba supported three massive compound nests, which included more than 200 chambers.

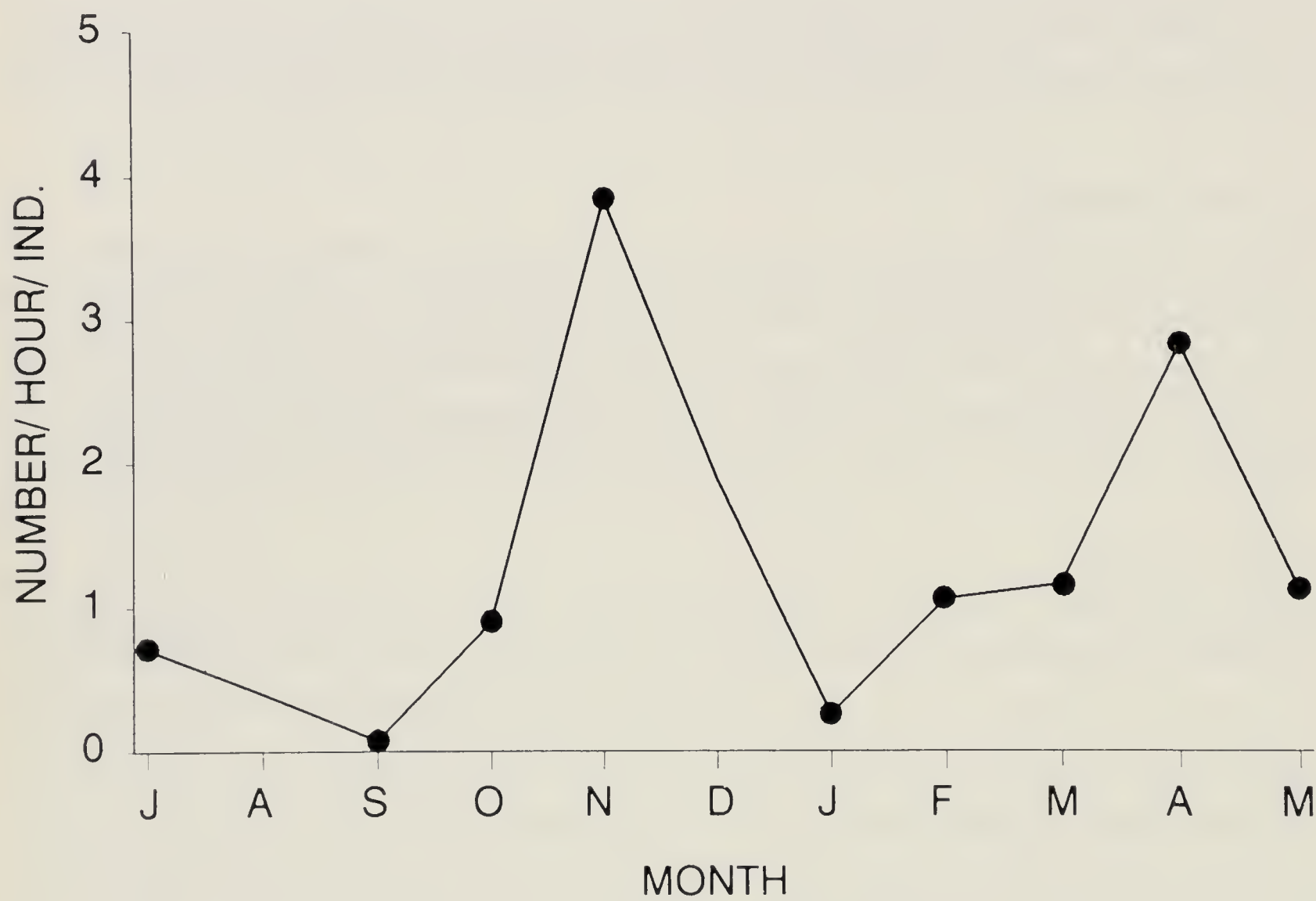


FIGURE 1 - Annual variations in the number of sticks being brought to the nest by Monk Parakeets (data from Martella and Bucher in press.).

Average nest size in our study area in Jesus Maria was small: 73% of the studied nests had only one chamber, 19% had two, 6% three, and 2% four (n= 123) (Navarro & Bucher unpubl. data). The high predominance of single-chamber nests may have been the consequence of previous nest destruction by the ranch owners. Lack of adequate support may also play an important role in limiting nest size. Strong winds and storms cause the falling of many nests. Larger nests appear to be more likely to fall than smaller nests.

In old nests parasites become very abundant (particularly the hematophagous cimicid bug *Psitticimex uritui*), which may pose a disadvantage for the long-term occupation of large nests. Monk Parakeets add green vegetable material to the lining of the nests during the breeding season, a behaviour that may help to control parasites (Bucher 1988). The parakeets also show low nest site fidelity which may be related to nest in-

festation: an average of 47% of the population changed nests between years, moving a mean distance of 500 m (Figure 2) (Martin & Bucher unpubl. data).

Breeding starts in October. Most of first eggs are laid during the second half of October and the first half of November. Non-breeding pairs usually occupy isolated nests or chambers in a compound nest.

Nestling growth rate is intermediate between that of open-nesting and cavity-nesting birds (per-day growth rate constant $K = 0.24$) (Navarro & Bucher 1990). Fledglings start leaving the nest about 40 days after hatching. On several occasions we observed that fledglings from neighbouring nests concentrated in one nest (creche) where they were fed by adults.

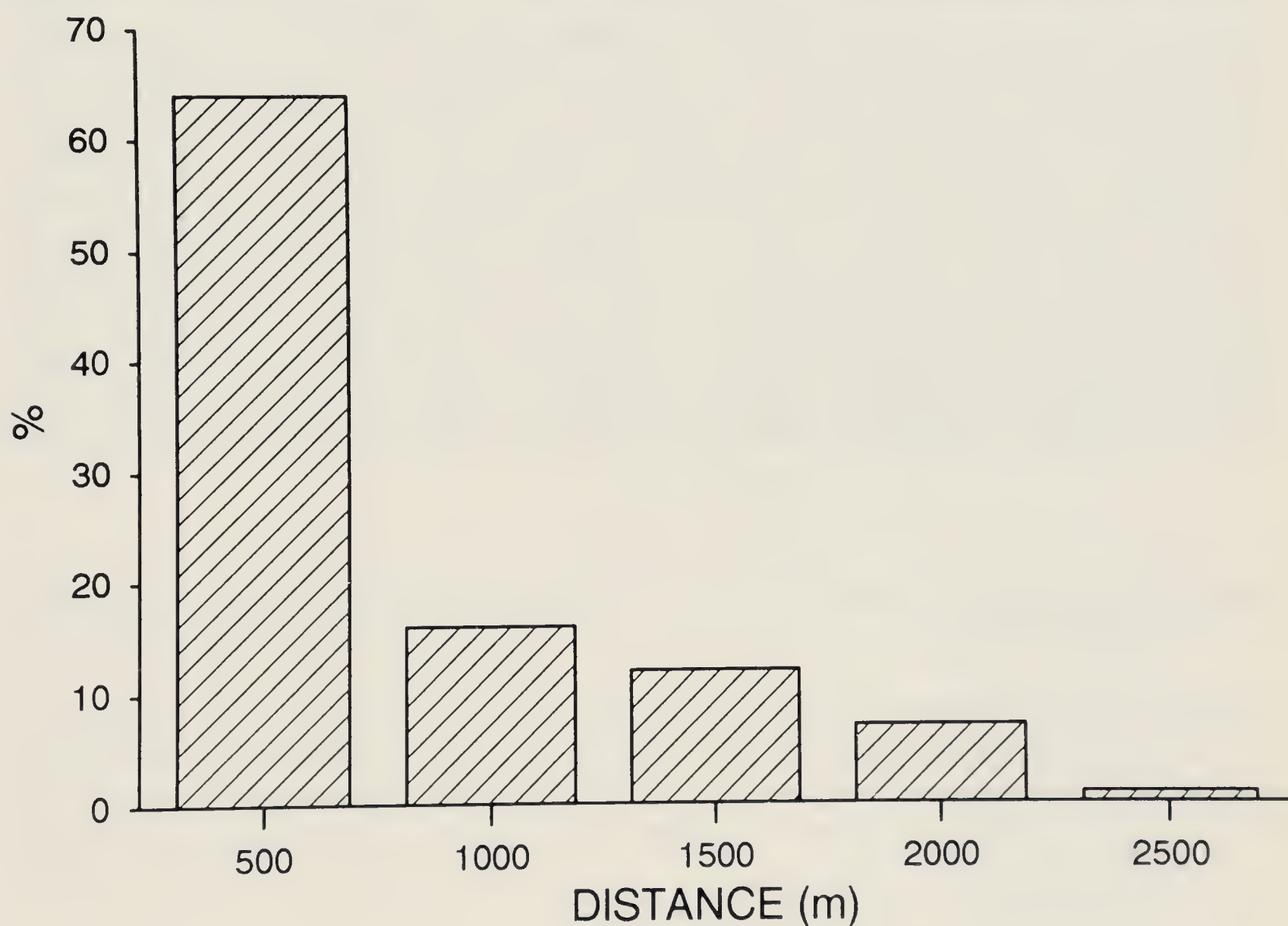


FIGURE 2 - Average distance moved by adult Monk Parakeets between censuses in our study area (data from Martin and Bucher unpubl. data).

After leaving the nest, fledglings remained with their parents for several months, but they always left the parental nest before the start of the following breeding season (Figure 3). Dispersal of juveniles from their nest of origin to their first breeding place was recorded for four juveniles. Dispersal distance was 300 m, 1250 m, 1400 m, and 2000 m (average 1230 m) (Martin & Bucher unpubl. data). However, this average may be an underestimation, given that our sampling area was limited and we did not have band recoveries besides our own. Helping at the nest, i.e. allofeeding siblings or other juveniles, was not observed as a regular event. However, we noticed a few incidental cases of allofeeding: older fledglings fed their younger siblings, a non-breeding trio fed fledglings from a neighbouring nest, and a breeding bird fed a begging juvenile

from a neighbouring nest. More sibling to sibling allofeeding could have taken place earlier inside the nest but could not be observed (Martella & Bucher unpublished data).

Basic demography

The Monk Parakeet population in our study area grew constantly during the first years and showed a tendency to stabilize in the last two years (Figure 4). This trend may have occurred because, until the initiation of our study, Monk Parakeets had been controlled by the ranch owners mostly by nest destruction. In any given year of our study period only a proportion of the adults bred, varying between 37% and 60% of the total.

The first clutch of the season ranged from one to 11 eggs, averaging 6.0 eggs, whereas replacement clutches had on average 5.0 eggs. Eggs were laid with an average laying interval between eggs of 2.1 days. The incubation period averaged 24 days. Replacement clutches after nesting failure were laid by 20% of the pairs, but only 7% of the successful pairs attempted to renest. On average 45% of the chambers fledged young, and annual productivity per breeding pair averaged 1.38, varying from 0.46 to 2.30. In total, 23% of the eggs laid fledged young. We did not find significant difference in pair productivity between colonies of different size, although productivity per pair was slightly higher in four-chamber colonies (1.58) than in those with three (1.33), two (1.33) or one (1.47) chambers; these differences were not significant (unpubl. data). However, our sample size of large nests was too small (only three four-chamber colonies) to allow us to raise definitive conclusions from our data.

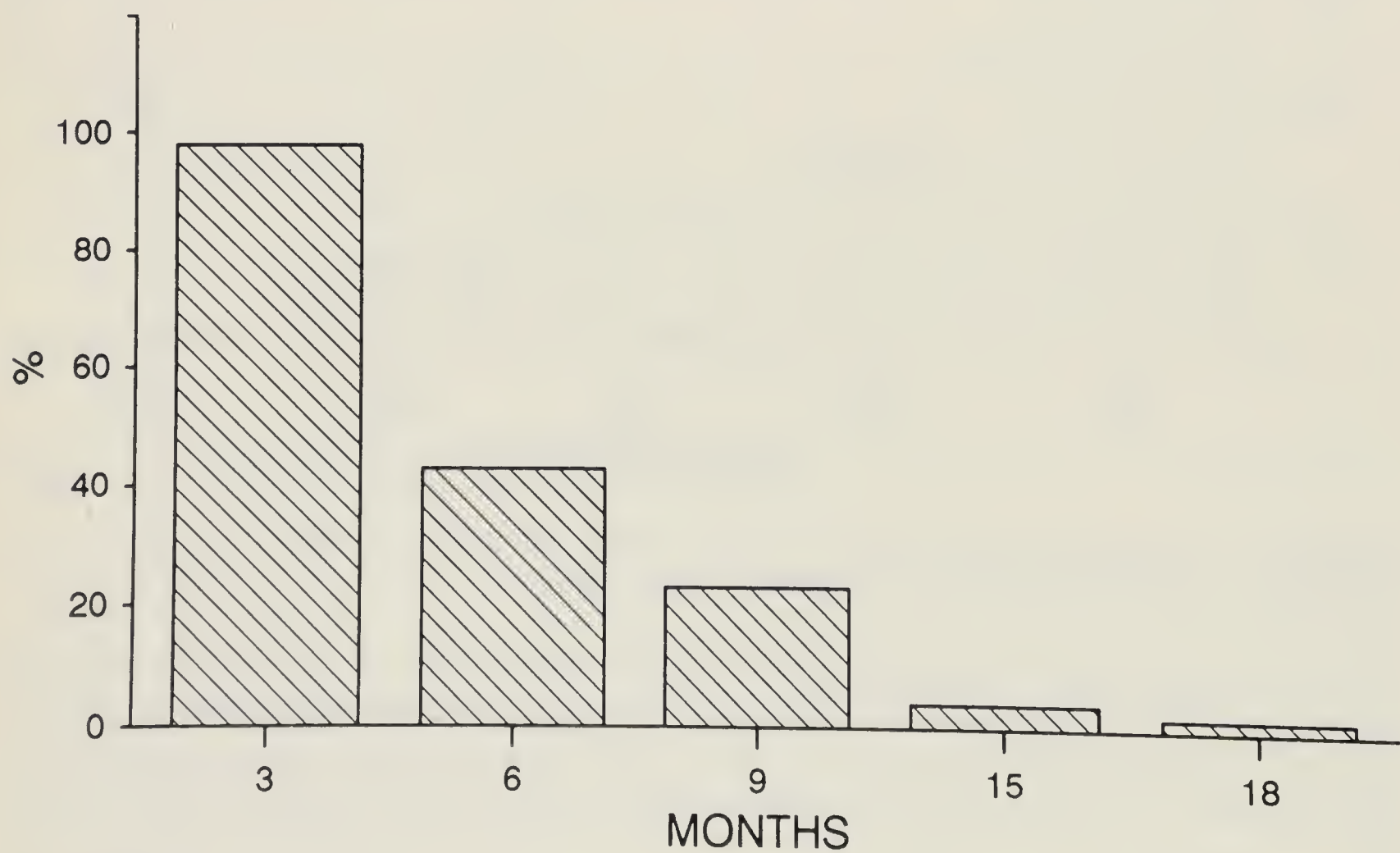


FIGURE 3 - Proportion of Monk Parakeet's fledglings remaining at the natal nest chambers at different ages in the study area at San Antonio Ranch. Notice that the following breeding season starts just after they become nine months old. In the few cases in which parakeets remained in their natal nest after that age their parents had already left the nest and bred elsewhere (see text) (data from Martin and Bucher unpubl.).

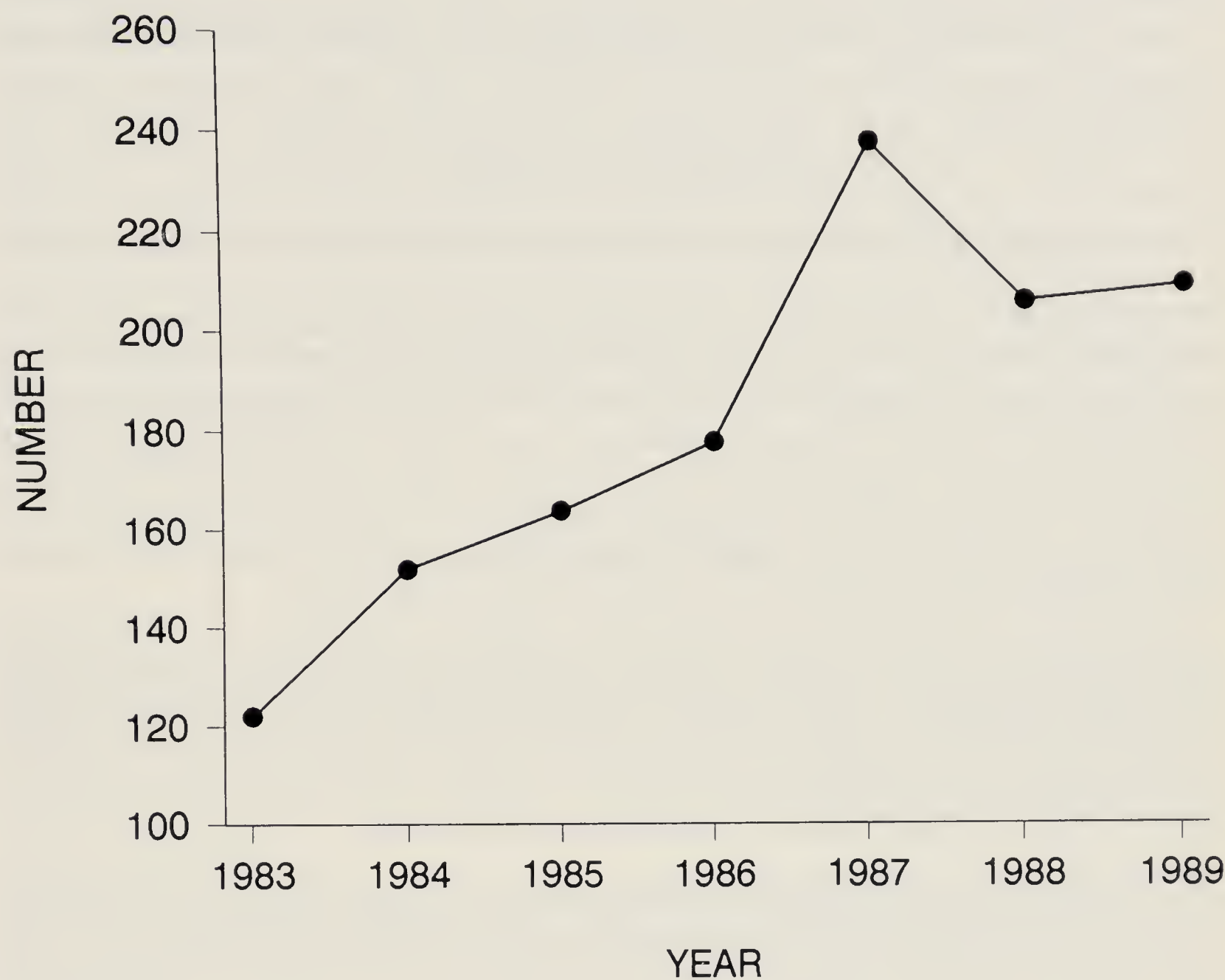


FIGURE 4 - Population of Monk Parakeets in the 604 ha study area at San Antonio Ranch, Jesus Maria, during the study period.

Annual survival of first year birds was estimated at 61%, whereas in adults it was 81% (Martin & Bucher unpubl. data). These figures do not separate mortality from emigration, but are useful for comparisons with other communal breeding species for which similar figures have been provided (see Stacey & Koenig 1990).

DISCUSSION

Communal breeding in birds is usually characterized by reduced dispersal, delayed breeding, and helping (Brown 1987). In our study area the Monk Parakeet showed delayed breeding, some degree of reduced dispersal, but only incidental direct helping by allofeeding. However, helping in nest building and maintenance, as well as vigilance of the compound nest, was a constant behavioural feature, although we did not find indications of productivity difference by nest colony size. Incidental cases of helping by allofeeding suggest a substrate for helping upon which selection could act should helping increase in adaptive value (Brown 1987). Further evidence supporting the existence of a potential for helping in Monk Parakeets comes from the observations made by S. Emlen (in press) on Monk Parakeets (of an unknown subspecies) breeding in an aviary, where some non-breeding individuals fed nestlings.

Delayed breeding maturity seems to be common in parrots and has been reported in the Puerto Rican Amazon *Amazona vittata* (Snyder et al. 1987), the White-tailed Black Cockatoo *Calyptorhynchus funereus* (Saunders 1982), and the Galah *Cacatua roseicapilla* (Rowley 1983), none of which are communal breeders. However, in the Green-rumped Parrotlet *Forpus passerinus*, a smaller sized species, 9% of the males and 56% of the females breed in first year of life (Beissinger and Bucher in press). This may suggest a direct correlation between size and delayed breeding in parrots.

Reduced dispersal has not been described in the published literature on other neotropical parrots, although current research on the Green-rumped Parrotlet in Venezuela has shown that most first nestings occur within 1 km of the natal nestbox (S. Beissinger, pers. comm.). Dispersal distance is over 20 km in the White-tailed Black Cockatoo (Saunders 1982) and the Galah (Rowley 1983), well over the average 1.2 km found in Monk Parakeets. Possible constraints on young Monk Parakeets from dispersing and becoming independent breeders may include the saturation of suitable nesting habitat and the energy costs of building large stick nests.

Habitat saturation does not seem to provide a general explanation for reduced dispersal in Monk Parakeets. In our study area nesting habitat was not limiting and the population continued to grow during the first part of our research, although it may be in part the result of past destruction of nests. However, habitat saturation may be an important factor in regions where nesting sites are limiting.

Even if breeding is not prevented by habitat saturation, reduced dispersal in the Monk Parakeet may be related to the high energetic cost of building and maintaining bulky nests. Because adding a nesting chamber to a compound nest requires less building effort and material than building a new nest, birds may benefit from decreasing energy and time expenditure by nesting in an already existing nest. Nesting in colonies may provide an opportunity for inexperienced birds to learn nestbuilding skills. Moreover, it is likely that birds could also benefit from communal guarding against predators, or the "selfish herd" (Hinde 1961) effect provided by members of the colony. However, continuous growth of a nest beyond a critical size may increase the risk of the whole structure falling.

Although we only found incidental helping in our study, it is possible that helping in natural conditions might be favoured under different circumstances, e.g. when dispersal is more difficult than was the case in our study areas (Emlen & Vehrencamp 1983). A greater difficulty in dispersing may occur in areas where nesting habitat becomes limiting as populations reach saturation levels, or where nesting habitat is very scarce, making dispersal highly risky. Finally, the possibility that different populations in each of the three different subspecies of Monk Parakeets may show differences in helping behaviour cannot be ruled out.

In conclusion, our results suggest that the Monk Parakeet breeding system shows some characteristics of a communal breeder, including reduced dispersal, delayed breeding, and signs of incipient helping (Brown 1987). However, given that there is little information on other South American psittacines, we cannot be certain whether this set of characteristics is unique to the Monk Parakeet or, on the contrary, is widespread among neotropical parrots. Further elucidation of the causes and consequences of the Monk Parakeet social system would require more detailed research

comparing populations under different ecological conditions and saturation levels, as well as comparative work with other neotropical members of the family.

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ANNUAL VARIATION IN PRODUCTIVITY OF NORTH ISLAND KAKA ON KAPITI ISLAND, NEW ZEALAND

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ABSTRACT. Productivity in North Island Kaka *Nestor meridionalis septentrionalis* on Kapiti Island, varied markedly between two breeding seasons. In 1988, 26 nests were recorded producing an average of 0.88 fledglings per pair, while in 1989 only nine nests were recorded producing 0.22 fledglings per pair. Starvation of nestlings was not observed in 1988, but was the primary cause of nest failure in 1989. As Kapiti Island lacks most of the introduced competitors now widespread on the main islands of New Zealand, this suggests that nesting in the Kaka is predominantly confined to years in which food is relatively abundant. Productivity in the Kaka may be more variable, and in the long-term, lower, than that of most other parrots due to its more variable, temperate environment.

Keywords: *Nestor meridionalis*, productivity, annual variation, food limitation, predation.

INTRODUCTION

The North Island Kaka *Nestor meridionalis septentrionalis* [nomenclature follows Kinsky (1970)] is a large (length = 430 mm; weight [maximum range] = 390 - 555 g, $n = 20$), omnivorous forest parrot endemic to New Zealand. Once widespread, the range of the Kaka has declined since European colonization (Buller 1888, Bull et al. 1985). The North Island Kaka is now considerably more abundant on a few offshore islands than on the North Island mainland (Oliver 1974, Bull et al. 1985). These islands are notable for their relative lack of the introduced mammalian predators and competitors now widespread on the New Zealand mainland (Atkinson & Bell 1973). While Kaka populations on the North Island mainland are predominantly confined to large remnants of mature native forest (Oliver 1974, Bull et al. 1985), the off-shore islands on which the bird remains common are relatively small, and the vegetation of one has been heavily modified by human-induced fires (Fuller 1985). In view of this, it would seem that introduced predators and competitors, rather than forest size or age, have been the primary factors in the decline of the Kaka on the North Island mainland.

In order to understand how North Island Kaka might be affected by introduced competitors and predators, it is necessary to obtain information on the birds' productivity. In the only available study of Kaka productivity, in South Island Beech *Nothofagus* sp. forest, Beggs and Wilson (1987, in press) found that only two of 31 radio-tagged birds attempted to breed in six years. The majority of nesting in this population appears to have been confined to one of the six years it was under study (J. R. Beggs pers. comm.). Such infrequent nesting suggests a productivity much lower than that recorded in other similarly sized parrots (Rowley 1980; Saunders 1982, 1986; Smith & Saunders 1986; Gnam 1991).

Infrequent nesting within populations is also known to occur in another New Zealand parrot, the Kakapo *Strigops habroptilus* (Best & Powlesland 1985, Moorhouse &

Powlesland in press) and in another New Zealand endemic, the New Zealand Pigeon *Hemiphaga novaeseelandiae*; (M. N. Clout pers. comm.). Other parrots (Rowley 1980, Gnam 1990, 1991) have occasional years when relatively few individuals nest. The available data on these three New Zealand species, however, indicate that most nesting occurs at infrequent intervals.

Introduced wasps *Vespula vulgaris* and *V. germanica* and the Australian brush-tailed possum *Trichosurus vulpecula*, an arboreal herbivore now widespread on the New Zealand mainland, probably had adverse effects on the productivity of the South Island Kaka population studied by Beggs and Wilson (1987, in press). Wasps compete with Kaka for Beech honey-dew, the sugar rich substance excreted by the scale insect *Ultracoelostoma assimile* (Beggs & Wilson, in press) and nectar. Possums are likely to compete with Kaka for fruit and nest cavities. Examination of Kaka productivity on an offshore island where the only introduced mammalian competitors are rats, and where wasps are less abundant, could provide a valuable comparison for such research on the mainland. This study sought to determine the factors influencing the breeding productivity of the Kaka on Kapiti Island.

STUDY AREA AND METHODS

Kapiti Island (2000 ha), a nature reserve administered by the New Zealand Department of Conservation, lies 50 km north of Wellington and 5.5 km off the North Island west coast. Virtually deforested by fire early last century, Kapiti Island is now predominantly covered by a variety of seral indigenous forest (Fuller 1985). Except for the Polynesian rat *Rattus exulans* and Norway rat *R. norvegicus*, the island is free of feral introduced mammals. The Australian brush-tailed possum, introduced to Kapiti Island in the 1890s, was finally eradicated in 1986. The introduced common and German wasps, competitors of Kaka in South Island beech forest (Beggs & Wilson, in press), are present on Kapiti Island but at much lower densities (pers. obs.).

All nest sites found were in tree-cavities, most within three metres of the ground and a high proportion actually at ground level (Table 1). While low (< 3 m), and particularly ground level nests appear common on Kapiti Island, the high number of such sites found probably also reflects the greater ease with which I was able to detect them. Most (14/20) nest sites within three meters of the ground were detected when hens flushed from the nest chamber, or by examining cavities in large (> 30 cm diameter at breast height) trees. Two advanced nests were located by the distinctive smell of nestlings' faeces. In contrast the five nests located above three meters height were found by the relatively time consuming process of observing courting birds.

Once found, I checked nests weekly using a bright light and an extendible angle mirror to determine final clutch size, hatching and fledging success. Climbing equipment was used to examine high nests. Because some nests were discovered long after hatching had occurred, or were destroyed by predators prior to hatching, I was not able to determine final clutch or brood size for all nests. Estimates of average clutch and brood size were, therefore, derived from the largest available subsample of the total found. Four nests in sites previously used within the same season were excluded from estimates of productivity because I could not determine whether these were nests of the previously observed pair or a new pair.

TABLE 1 – Height of Kaka nest sites found on Kapiti Island in 1988 and 1989. Mahoe = *Melicytus ramiflorus*, Kohekohe = *Dysoxylum spectabile*, Pukatea = *Laurelia novazelandiae*, Kamahi = *Weinmannia racemosa*, Rata = *Metrosideros robusta*, Puka = *Griselinia lucida*.

height range (m)	Tree species						Dead tree	Total
	Mahoe	Kohekohe	Pukatea	Kamahi	Rata	Puka		
<0-0	7	3	0	0	0	0	0	10
0-1	1	1	0	0	1	0	0	3
1-3	2	3	0	0	0	1	1	7
3-5	0	1	0	1	0	0	0	2
5-7	0	0	0	0	0	0	0	0
7-9	0	0	1	0	0	0	0	1
9-11	0	1	0	0	0	0	0	1
11-13	0	0	1	0	0	0	0	1
Total	10	9	2	1	1	1	1	25

RESULTS

Kaka pairs on Kapiti Island laid an average of 3.71 eggs (95% confidence interval = 3.35-4.07, n = 24, range = 1- 5), hatched an average brood of 2.09 chicks (95% confidence interval = 1.64 - 2.54, n = 23, range = 0 - 4), and, if their nest did not fail completely, fledged 1.69 young (95% confidence interval = 1.18 - 2.21, n = 13, range = 1- 3) (pooled data from 1988 and 1989). The low brood size relative to the number of eggs laid appeared primarily due to poor hatching success. Hatching success in 1988 was 58% (35 chicks from 60 eggs in 16 nests) and 52% (13 chicks from 25 eggs in 7 nests) in 1989, giving an overall value for both years of 56% (48 chicks from 85 eggs in 23 nests). Both 100% and 0% hatching success were rare, occurring in only two and three clutches respectively. Examination of 16 unhatched eggs revealed 13 to be infertile and three to contain dead embryos.

In the 1988 breeding season I located twenty-three active Kaka nest sites, three of which were reused in the same season giving a total of 26 actual nests (Table 2 & 3). Despite being more experienced in detecting nests, and making a greater search effort (36 days searching for nests in 1989 against 24 days in 1988), in the 1989 season I only found eight active sites, one of which was reused within the same season (Table 2 & 3). All but two of the nest sites found in the 1989 season had been used the previous year. Nine of the 17 1988 nest sites not used in 1989 had been successful while three of the six 1988 sites reused in 1989 had been unsuccessful in 1988.

Pairs that did nest in the 1989 season produced an estimated 0.25 fledged young per pair (95% confidence interval = 0.14 - 0.64, n = 8) as opposed to 0.87 fledged young per pair (95% confidence interval = 0.64 - 1.10, n = 23) in the 1988 season (Table 2). Considering pairs which fledged young only, the only two successful nests in the 1989 season produced only one fledgling each while successful pairs in the 1988 season produced an average of 1.82 fledglings per pair (95% confidence interval = 1.23 - 2.4, n = 11) (Table 2).

TABLE 2 – Productivity of Kaka on Kapiti Island in 1988 and 1989

	No. active nest sites	No. young fledged	No. fledglings per pair	No. fledglings per successful pair
1988	23	20	0.87	1.82
1989	8	2	0.25	1.00
Total	31	22	0.71	1.69

TABLE 3 – Fate of Kaka nests on Kapiti Island in 1988 and 1989

	Preyed on by			Weka	Abandoned Infertile	Flooded	Starved	Fledged	
	Total	Rat	Morepork						
1988	26	6	3	1	2	1	1	0	12
	%	23	12	4	8	4	4	0	46
1989	9	2	0	0	0	2	0	3	2
	%	22	0	0	0	22	0	33	22
Total	35	8	3	1	2	3	1	3	14
	%	23	9	3	6	9	3	9	40

Considering all nests found, 46% were successful in the 1988 season and only 22% in the 1989 season (Table 3). In 1988, rat predation of nestlings was the single greatest cause of nest failure accounting for the loss of 23% of nests found (Table 3). In the 1989 season, however, starvation of nestlings was the primary cause of nest failure, accounting for the loss of 33% of nests (Table 3). Starvation was the presumed cause of death when chicks were found dead without sign of injury. Such chicks were always in nests containing more than one young and in all cases the younger nestlings died first. The two successful nests in the 1989 season each had only one chick hatch.

Overall, in both seasons, only 40% of nests succeeded (Table 3). Rat predation was the predominant cause of nest failure accounting for the loss of 23% of nests found (Table 3). Rat predation was identified using the experimental observations of Moors (1978) who found that rats typically ate eggs and nestlings in situ, leaving remains in the nest. Where eggs and nestlings disappeared without trace, the Morepork *Ninox novaeseelandiae*, a native owl, or the Weka *Gallirallus australis*, an endemic rail, were assumed to be the predator. Seven of the eight nests preyed on by rats had an opening to the nest chamber within 20 cm of the ground, while the other was in a leaning tree which afforded easy access. Only 6% (1/17) of nests in sites over one metre above ground were preyed on by rats. In contrast, 50% (9/18) of nests in sites within one metre of the ground were preyed on by rats.

DISCUSSION

The productivity of successful pairs of North Island Kaka on Kapiti Island over two years is consistent with the available data on other large parrots in terms of small clutch size and the small number of young fledged. The low hatching success of Kaka on Kapiti Island (56%), however, appears more unusual. Smith and Saunders (1986) found 75-100% hatching success in four species of Australian parrots but recorded a comparable 65% hatching success in the Red-tailed Black Cockatoo *Cacatua magnificus*. Gnam (1991), however, also recorded a hatching success of 56% in the Bahama parrot *Amazona leucocephala bahamensis* on Great Abaco Island. Gnam (1991) found all eggs examined to be fertile. However, 81% (13/16) of the unhatched Kaka eggs I examined were infertile and only 19% (3/16) contained dead embryos.

The difference in the number of active nest sites found in 1988 and 1989 suggests that long-term productivity in Kaka could be lower than in most other parrots. While the infrequent nesting of South Island Kaka observed by Beggs and Wilson (1987, in press), could reflect competition from introduced wasps and possums, productivity in the 1989 season on Kapiti Island appeared low in the absence of possums, and probably with no significant increase in competition from wasps. It is possible that I found fewer nests in 1989 because some pairs which had failed nests the previous year renested the following year in sites more difficult to detect. However, this seems unlikely as over half the nest sites not used in 1989 had been successful the previous year. The fact that captive Kaka nest, and even reneest, every year (M. Sibley pers. comm.) indicates that Kaka can breed annually given adequate food resources. In view of this, the far fewer nests found in 1989 suggests that food was less abundant for the birds in that year.

While I have no comparative data on food availability for Kaka in 1988 and 1989, the high incidence of starvation of nestlings in 1989 supports this food limitation hypothesis. The only two pairs which successfully fledged young in 1989 each had only one chick, whereas successful pairs in 1988 were able to fledge an average of 1.82 chicks. Fruiting in many species of forest trees, including those with fruits taken by Kaka, was more abundant and prolonged in the 1988 than 1989 season (pers. obs.). New Zealand Pigeons, which are predominantly frugivorous in the breeding season (M. N. Clout pers. comm.), also displayed markedly greater productivity on Kapiti Island in 1988 than 1989 (pers. obs.).

Clutch and brood size in many temperate birds often varies in response to annual variation in food availability (Cody 1971). In the Kakapo (Best & Powlesland 1985; Moorhouse & Powlesland in press) and New Zealand Pigeon (M. N. Clout pers. comm.), most individuals only nest in relatively infrequent years that are presumably more favourable for breeding. My data, and that of Beggs and Wilson (1987, in press) suggest that the Kaka is similar. The likely longevity of these species, long period of dependency of young, and the former absence of mammalian nest predators in New Zealand, may all have favoured not nesting in years in which conditions are less suitable, rather than reducing clutch or brood size. In effect, these birds could be said to reduce their clutch size to zero in less favourable years.

If productivity in Kaka is limited by the availability of plant foods even in the absence of significant competition from introduced species, then the latter are likely to have a

significant negative effect on the birds. Kaka may only be able to breed in the presence of competitors in habitats where suitable plant foods become periodically superabundant. Kaka in South Island beech forest appear to depend on the infrequent mast seeding of red beech *Nothofagus fusca* for successful breeding (J. R. Beggs pers. comm.). As years of high productivity in Kaka could, even in the absence of competitors, be infrequent, Kaka populations may be particularly vulnerable to introduced predators.

On Kapiti Island, rat predation was predominantly confined to nests within a metre of the ground. This suggests that the predominantly ground-foraging Norway rat was the main predator of nestlings rather than the more arboreal Polynesian rat (Atkinson 1985). As I was probably biased toward detecting such low nests, I have probably overestimated the impact of rat predation on Kaka productivity on the Island. Nonetheless, as 50% of nests within one metre of the ground were destroyed by rats, the latter clearly have a significant effect on the productivity of the nest sites accessible to them. In a mainland population, all nests would be vulnerable to arboreal predators such as ship rats *R. rattus* and stoats *Mustela erminea*, irrespective of height. Stoats are capable of killing female Kaka on the nest (Beggs & Wilson, in press), and so could have a far more immediate effect on productivity than rats.

In conclusion, nesting in Kaka on Kapiti Island appears limited by annual variation in plant food availability even in the absence of most introduced competitors present on the mainland. This suggests that the latter may have a significant negative effect on Kaka productivity. Introduced competitors may have already restricted Kaka to habitats where important plant foods become superabundant with sufficient frequency. Such populations are, however, likely to nest infrequently. High levels of nest predation could thus significantly reduce the long-term productivity of such populations. Thus, while introduced competitors may have reduced the range of habitats in which the Kaka can breed successfully, mammalian nest predators may now pose the most immediate threat to the continued survival of the species. Supplementary feeding of Kaka populations may be an effective management technique to increase their productivity.

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CONCLUDING REMARKS: SYMPOSIUM ON THE ECOLOGY AND SOCIAL BEHAVIOUR OF PARROTS AND PARAKEETS

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After a long history of little scientific research, progress is being made in research on the members of this interesting group of birds. In this symposium, Saunders showed how the sympatric Carnaby's and Red-tailed Black Cockatoos have responded differently to the same changing environment and examined the factors responsible for those different inter-specific responses. Even though the Red-tailed Black Cockatoo population is increasing in the wheatbelt of Western Australia, Saunders found that its reproductive rate is very low for a species laying only one egg per breeding season. A low reproductive rate may not have posed problems for a long-lived species in a stable environment, but in the rapidly-changing environment of Western Australia, the long-term prospects for such a species are grim, particularly so if no conservation areas are set aside for such nomadic species.

Since most psittacines live in flocks outside the breeding season, Arrowood's interest was in analyzing the patterns of interaction within flocks. Using captive flocks of the Neotropical Canary-winged Parakeet, she found patterns of social interaction that, if confirmed in other psittacines, would be different from that of any other bird group. In the Canary-winged Parakeet, affiliative interactions within the pair are egalitarian, with reciprocal allopreening and allofeeding. Affiliative interactions do not extend outside the pair relationship (except to offspring), and males do not seek sexual activities with nonmate females. Aggressive acts by each sex are distributed equally to same-sexed and oppositely-sexed individuals. The only significant unilateral tendency was for males to have higher rates of aggressive acts to males than females did to males. It would be interesting to compare the patterns of interaction found in monomorphic and monochromatic species with those of dimorphic or dichromatic species to see if monomorphic species are more egalitarian in their behaviour.

Two of the symposium papers (Gnam, Moorhouse) dealt with the basic biology of large parrots living on small islands. Since both species are declining, such basic information is essential for the preparation of preservation and management strategies. The survival of species on small islands is usually tenuous; in the face of human manipulation of the environment, the chances for continued survival plummet. The Bahama Parrot (Gnam) relies on three plant species for 74% of the food fed to chicks. Similarly, the Kaka (Moorhouse) uses hard-to-obtain insect larvae and unpredictably-fruiting and flowering plants for the food fed to chicks. On such small islands the birds have few other choices. On top of a precarious situation because of food supplies, chicks are lost to introduced mammals. Cats prey on chicks in subterranean nests

used by the Bahama Parrot and Norway rats take eggs and chicks in near-ground nests of the Kaka. Ground nesting implies an adaptation to the absence of suitable arboreal nest cavities, a situation uncommon in psittacines. Nesting success in the subterranean-nesting Bahama Parrot was lower than that of the arboreal cavity-nesting congeneric Hispaniolan Parrot and Puerto Rican Parrot. In the Kaka, however, nesting success on the island may be greater than that on the mainland. If predators could be removed and the islands maintained predator free, they might provide a salvation for the parrots.

Bucher et al. presented data on many interesting aspects of the Monk Parakeet's social life and population biology. The Monk Parakeet is the only psittacine to fabricate its own nest which it makes of sticks and twigs. This species may be in the incipient stages of the evolution of a communal breeding system, a system not recorded in any other psittacine. The stick nests that are constructed may be occupied by a single pair or by multiple pairs; non-breeding individuals may also occupy nest chambers. All occupants of a compound nest participate in its construction, maintenance and defense. Older siblings and nonbreeding and breeding neighbours were observed allofeeding young. The Monk Parakeets had a large clutch size, but low productivity per breeding pair. There was some suggestion that productivity might be higher the greater the number of chambers per compound nest. The highly-visible nest of these parakeets facilitates their destruction by the agricultural community which considers them a pest. On the other hand, population expansion is occurring into areas where recently-introduced tall eucalyptus trees provide attractive substrates for the large compound nests.

There are many questions still unanswered about psittacine behaviour and ecology. No one has yet explored whether vocal mimicry plays a role in the natural life of those species with that incredible ability. The life-long, year-round, highly exclusive monogamy of many psittacines represents an extreme case among the many avian variations on the monogamy theme, but it has received little theoretical or empirical attention. Since most psittacines are not territorial, many interesting questions exist about the patterns of their flock movements relative to the patterns of abundance of food sources and competition with other species. The study of these distinctive birds will allow us to test the robustness of current principles of avian ecology and behaviour.

SYMPOSIUM 9

BIRD FLIGHT

Conveners G. E. GOSLOW and I. D. HUMMEL

SYMPOSIUM 9

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INTRODUCTORY REMARKS: BIRD FLIGHT

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Bird flight as a mode of locomotion has held us in fascination for centuries. Studies by biologists and engineers have given us some explanation concerning the reasons for wingtip slotting, wing kinematics, and adaptive wing shapes, but many problems remain. At the 17th Congress (1978) in Berlin, Germany, as well as at the 18th Congress (1982) in Moscow, USSR, Professor Oehme from East Germany and Professor Nachtigall from West Germany were the convenors for sessions on bird flight. At the last 19th Congress (1986) in Ottawa, Canada, unfortunately no session on our topic took place. Therefore the Scientific Programme Committee of the present 20th Congress (1990) in Christchurch, New Zealand, voted for the organization of a symposium on "Bird Flight".

We were charged by the Scientific Programme Committee of the Congress to bring to the non-flight specialist a collection of papers that in addition to providing a review, would highlight current issues in bird flight and stimulate students for further study. We believe the selection of papers herein accomplish this charge.

WAKE STRUCTURE AND FORCE GENERATION IN AVIAN FLAPPING FLIGHT

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ABSTRACT. The mechanics of flapping flight have moulded the flight adaptations of birds, and are subject to a wide range of aerodynamic constraints. Flow visualization experiments and high-speed cinephotography have identified two 'gaits', distinguished by the upstroke and the variability of force generation (visualized in the wake vortices) typical of steady flight. In the vortex ring gait - used in slow flight and by birds with low aspect ratio wings - the upstroke is inactive; in the continuous vortex wake gait - in longer-winged birds in fast flight - the wake is a pair of undulating trailing vortices, and the wing deforms only slightly during the upstroke. The vortex ring gait demands intense activity of the supracoracoideus, but in the continuous wake gait this muscle may be unimportant. Theoretical models based on these experiments can predict a range of quantities relevant to flight, including mechanical flight power, and wing root bending moments, and these provide methods of testing the models.

Keywords: Birds, bats, aerodynamics, flapping flight, flow visualization, vortices, wingbeat kinematics, gait, flight power, efficiency.

INTRODUCTION

Flapping flight is a demanding adaptation. It demands much, not only from the wings and skeleton to meet aerodynamic stresses and from the physiological system to provide sufficient energy flows, but also from the scientist who attempts to study the mechanics of the movement of birds. Until recently much of what we know about flapping flight has been based on conventional aerodynamic theories, and on analogies and parallels with fixed-wing aircraft. While this approach has been of enormous importance, and retains fundamental significance for our understanding of flight mechanics and the aerodynamic design of birds, it is inevitably limited in application to natural flight: the wings of aircraft are not flapped. In aircraft, force generation is steady and continuous, while in flapping flight lift and drag forces vary in strength and direction during the wingbeat. In aircraft horizontal (thrust) and vertical (lift) forces are generated by essentially independent mechanisms - aerofoil lift from the wings, and thrust from jet or propeller engines - but birds have only aerofoil action for both lift and thrust. At this point the analogy with aircraft practice breaks down.

AERODYNAMICS

Aerofoil action and force generation

The wings of aircraft and of flying animals act as aerofoils. When held at the appropriate angle to the incident airflow, the tapered, asymmetric profile induces vortices bound onto the wing and trailing from the wingtips (trailing vortices are visible as the vapour trail behind high-flying aircraft); this vortex system forces air downwards behind the wing, and the wing experiences the reaction of this momentum flow as *lift*. Lift acts at right angles to the direction of movement of the wing, and is proportional to the speed of the wing and the strength or *circulation* of the bound vortex.

Lift is the largest aerodynamic force, but there are also three components of *drag*, reflecting friction and surface pressure on the body (*parasite* drag) and wings (*profile* drag), and the energy cost of generating the wake vortices (*induced* drag); drag is largely horizontal, and retards movement through the air.

Thrust from flapping wings

Animals must use aerofoil lift both as weight support and as thrust to overcome drag. With wings outstretched lift is fully capable of supporting weight, but there is no thrust, and the animal must be a glider, losing height as energy is expended against drag. Flapping is the mechanism by which a bird is able to sustain level flight using lift alone. *It is to provide a horizontal thrust to balance drag that animals must flap their wings.*

Flapping flight must be modelled as a means of configuring the wingbeat so that on average lift provides both a mean thrust and weight support. The primary movement of the wing is dorso-ventral flapping. As the wing moves downwards it also moves forwards relative to the air, and lift is inclined forwards, acting both as weight support and thrust; this is the main part of the wingbeat, and generates the bulk of the aerodynamic force. Symmetric flapping with upstroke in the same configuration as downstroke gives no mean thrust, since an upstroke with an aerodynamically active wing - while supporting weight - would generate a negative thrust, cancelling that from the downstroke. Down- and upstrokes must be asymmetric, with less lift in the upstroke either by a smaller wing planform or weaker bound vortex. The extent to which up- and downstrokes are asymmetric depends on the magnitude of the required thrust; this is a non-trivial problem, since thrust must balance drag, and drag depends in turn on lift and on wingbeat geometry and kinematics.

Vortex action in flapping flight

Whenever an aerofoil generates lift it sheds vortices, which in strength and location are symptomatic of the action of the wing. A trailing vortex is shed from the wingtips, equal in strength to the vortex bound on the wing. A transverse vortex is shed along the trailing edge whenever the bound circulation changes strength. Without the vortex wake there could be no momentum flow away from the bird, and hence no lift. Generation of the vortices represents a significant energy cost (induced drag); some authors claim that the bird could avoid this cost by eliminating all wake vortices, but then there would be no lift, and flight would be impossible. The vortices should be generated as efficiently as possible: the induced drag depends critically on vortex structure; wakes comprising closed circular loops or near-linear elements are most efficient in transporting momentum for minimum energy. I shall describe below that these are the only structures observed in birds in steady flight.

Visualization of the wake vortices is therefore a powerful means of clarifying force generation mechanisms in flight. The wake is a transient, three-dimensional structure, and experimental determination of its structure has been difficult. Initial observations of wake vortices in slow-flying pigeons (Magnan et al. 1938) and small fringillid passerines (Kokshaysky 1979) revealed a series of circular vortex rings, each formed by a single downstroke. This implies that all aerodynamic force was generated during the downstroke, and that the upstroke was mechanically passive, as predicted by my initial theoretical model of flapping flight (Rayner 1979, 1980); subsequent experiments and observations have, however, revealed that the vortex ring is not the only wake observed in birds.



FIGURE 1 — The wake of a Pigeon *Columba livia* in slow flight at approx. 3 m/s, showing a photograph of a single vortex ring, and a reconstruction of the air movements and position of vortex cores. (From Spedding 1982.)

Our flow visualization technique developed consists of seeding the air with neutrally buoyant soap bubbles filled with a helium-air mixture, which follow any movements of the air; we obtain an instantaneous 3-D view of the wake by photographing in stereo, with a series of flash guns (Figures 1-4). The bubble traces are longer and more curved when the bubbles are close to the vortex cores, and hence the position and strength of the vortices are determined. Unfortunately the technique reveals little of the airflow around the wings or of the formation of the trailing vortex cores close behind the wings.

First results confirmed Kokshaysky's vortex ring wake in Pigeon *Columba livia* (Figure 1) and Jackdaw *Corvus monedula* in very slow flight (Spedding 1986, Spedding

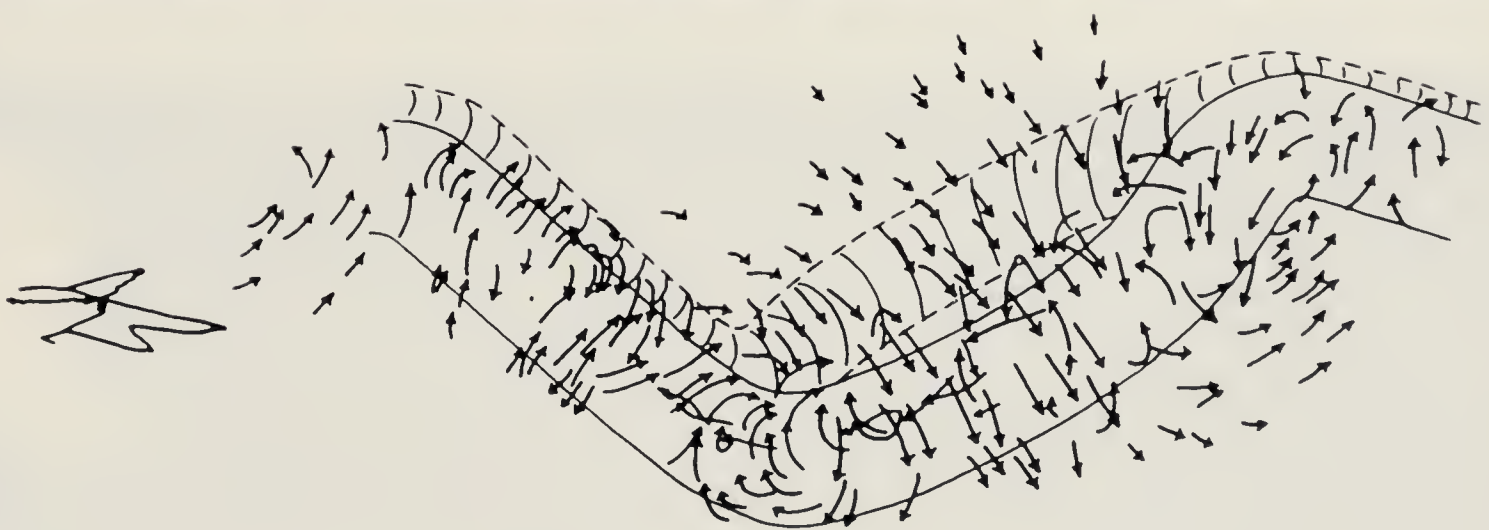


FIGURE 2 - The wake of a Kestrel *Falco tinnunculus* in normal flight at approx. 7 m/s. (From Spedding 1982.)

et al. 1984, see also Rayner 1986, 1988a). Transverse vortices are shed as the wing begins to generate lift at the start of the downstroke, and as it ceases lifting at the end of the downstroke. These join with the trailing vortices to form a toroidal vortex ring.

Measurement of the vortex size and strength showed that the rings carried only two-thirds of the momentum needed to support the bird's weight for one wingbeat (Spedding et al. 1984). This suggested, disturbingly, that some unconventional unsteady mechanism was generating significant aerodynamic force, yet theoretically all momentum should be visible in the wake. Subsequent measurements of body acceleration have shown the Pigeon followed a parabolic flight path, decelerating at approximately 0.3 g (J.M.V. Rayner & A.L.R. Thomas, in prep.).

The momentum discrepancy arose because the rings were smaller than expected, rather than weaker, and limits to the bound circulation on the wings may prevent the bird from balancing all of its weight in very slow flight.

A very different wake was observed in the European Kestrel *Falco tinnunculus*. In gliding the wake is a pair of straight line vortices similar to those generated by an aircraft wing (Spedding 1987a). In cruising flight (Figure 2) the upstroke is now aerodynamically active; no transverse vorticity is visible at any phase, and the vortices undulate following the path of the wingtips (Spedding 1987a, b, see also Rayner 1988a). Vortex strength is constant along the wake (as would be expected with no transverse vorticity), and is sufficient to support the weight: the bird controls wing pitch so that bound circulation remains constant, and ensures a net thrust by sweeping the wingtip back at the wrist during the upstroke so that the effective wingspan - the spacing between the vortex cores - is reduced (Rayner 1986, 1988a).

To investigate whether these two wake patterns were representative we have undertaken a survey of the wake patterns in a range of bird and bat species (Rayner, Jones and Thomas 1986, Rayner 1987, 1988a, Rayner & Thomas, in prep.); all fall into one of the same two patterns. In slow flight in all species studied (Pigeon, Jackdaw, Tawny Owl (Figure 3), Barn Owl, Cockatiel, Starling, Zebra Finch, Canary, Blackcap, etc.), and in cruise in slow-flying, broad winged species and in those using bounding flight (fringillid passeriforms, Budgerigar, Little Owl, Quail, Long-eared Bat, Pipistrelle Bat) the wake is vortex rings. In fast flight longer-winged species (Kestrel, Pigeon, Cockatiel, Noctule Bat, Dog-faced Fruit Bat, Swift, Swallow) adopt the continuous vortex wake. Transverse vortices are only observed with the vortex ring wake, and the 'ladder' wake of Pennycuik (1988) apparently does not exist in vertebrates (although it may be present in insects (Rayner 1986)). The absence of transverse vortices is not surprising, since the interaction of transverse vortices with the vortex on the wing can dramatically increase induced drag (Rayner 1986).

We have limited information about wake transitions in accelerating flight in a number of species including the Noctule Bat (Rayner et al. 1987), the Cockatiel and Meyer's Conure *Polioptila meyeri* (Figure 4). In transitions there is a single upstroke with circulation reduced compared to the subsequent downstroke. In each case the animal appears to have a critical speed at which gait is changed: the transition is rapid, within a single wingbeat, and at the same time wingbeat kinematics alter as amplitude and frequency both reduce. In decelerating flight the situation appears to be different, birds maintaining the continuous vortex wake down to low speeds during rapid deceleration just prior to landing; there may be advantages in stability and control from maintaining a lifting upstroke.

Wingbeat kinematics and gait

Patterns of wingbeat kinematics in flying birds have been studied by many authors (see Rayner 1988a), mainly by high-speed cinematography. The patterns observed are complex and varied, but can be simplified when kinematics are used as diagnostic of the aerodynamic function of the wings. Our flow visualizations support classification of wingbeat into clearly defined categories or *gaits*, associated with flight speed and with wing morphology, and distinguished by the function of the upstroke (see above, also Scholey 1983, Rayner 1988a). I use the term gait by analogy with terrestrial locomotion to refer to the pattern of movements of the limbs at different speeds

and in different types of flight; unlike the terrestrial parallel, transitions between flapping gaits may be gradual, and need not show the catastrophic discontinuities found in running tetrapods (Alexander 1989).

In flapping flight there are strict constraints on the aerodynamic action of the wing during the wingbeat, and hence on gait. At any speed aerodynamic factors demand a particular set of kinematics to ensure that mean lift, weight and drag are in equilibrium and that mechanical energy is minimum. The gait must be consistent with the mechanical properties and physiology of the muscles, because vertebrate muscles contract most efficiently only over a relatively narrow range of contraction strains (related to wingbeat amplitude) and strain rates (related to frequency); adequate safety factors must also be maintained in the structures of the pectoral girdle and the wing. We do not know how strict these constraints on gait can be, and they may be sufficiently inflexible for birds to be seriously constrained in selection of gait.

The vortex ring gait

The Pigeon (Figure 5a) shows typical wing movements of slow flight. In the upstroke the wing is strongly flexed, and the wingtip is brought close to the body to minimize profile drag and inertia. This phase is aerodynamically inactive (Rayner 1979), generates no lift, and the wake is formed of vortex rings generated solely during the downstroke, when the wing remains almost flat and fully stretched. As the upstroke has little aerodynamic significance, the detailed geometry of wing deformation is unimportant, and it is not analysed in detail.

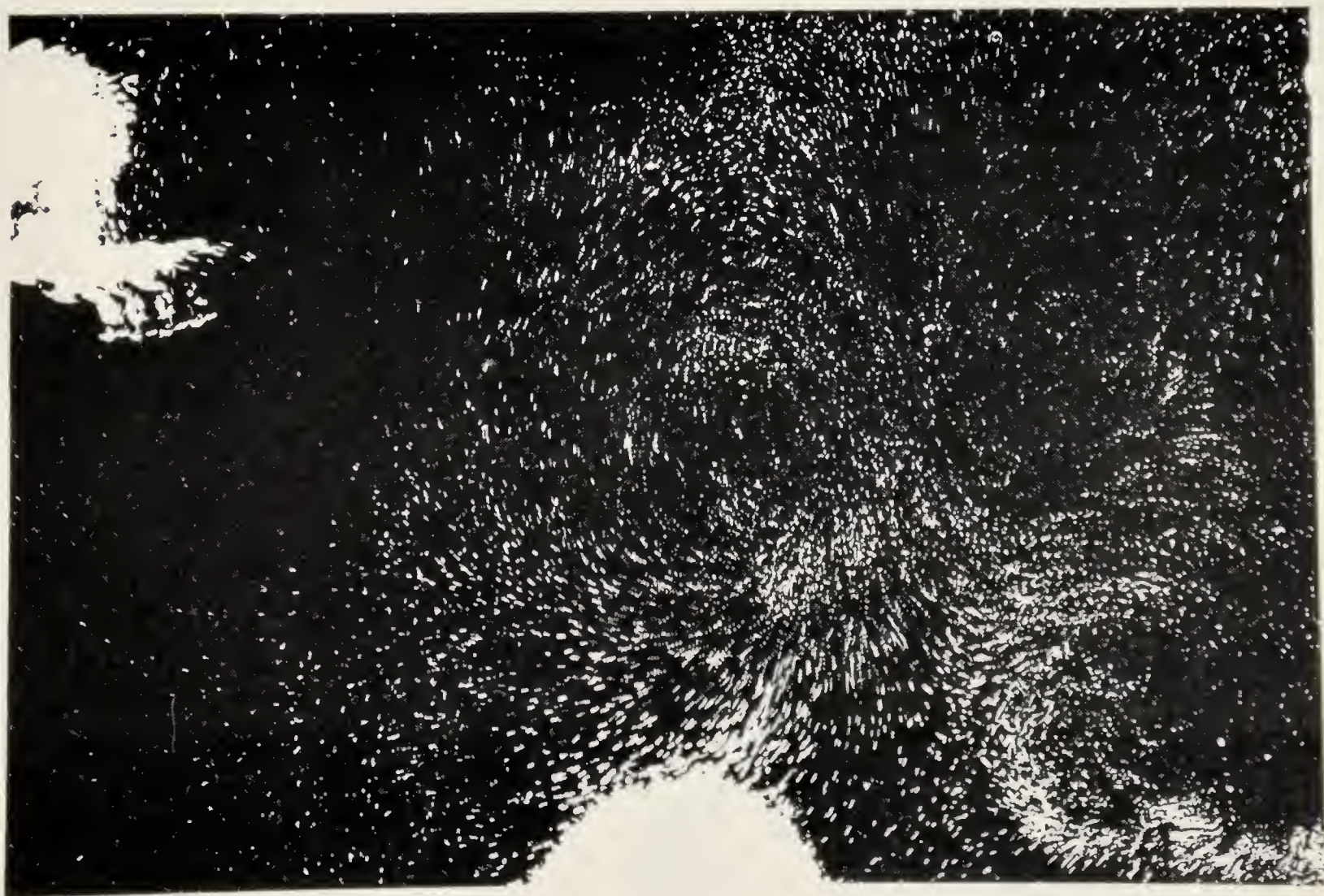


FIGURE 3 - The wake of a Tawny Owl *Strix aluco* in steady slow flight at approximately 2.5 m/s. Two vortex rings are visible. In each ring the stopping vortex is clearly defined, but the starting vortex is more diffuse; this may reflect a delay in vortex strength development at the start of the downstroke. (Photograph A.L.R. Thomas.)

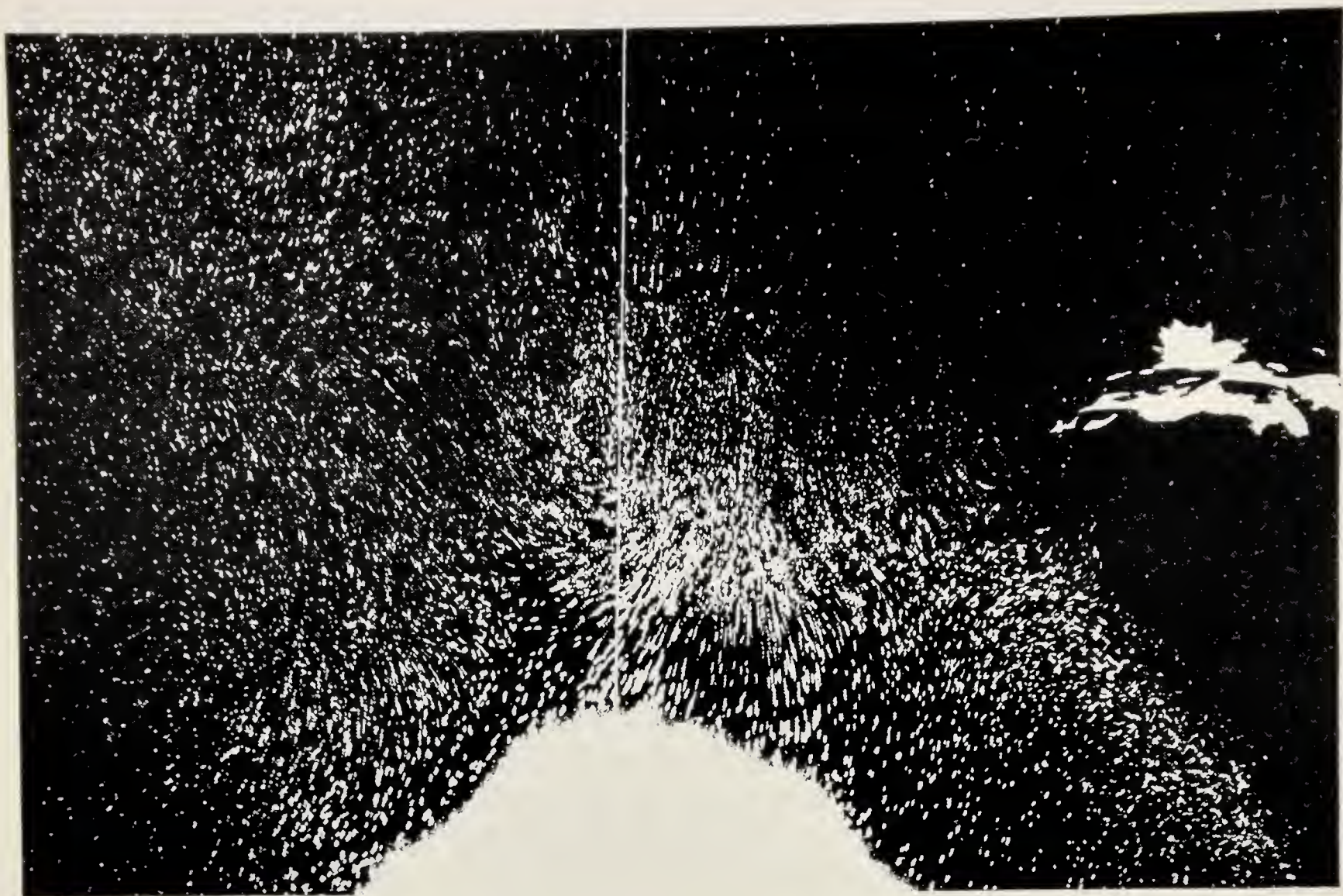


FIGURE 4 - The transitional wake in accelerated flight of Meyer's Conure *Policephalus meyeri*. To the left of the image the wake is a vortex ring; this is followed by a weak transverse vortex and a lifting upstroke, followed by another transverse vortex before the continuous vortex wake begins with a downstroke. The bird is in the middle of the following upstroke. (Photograph A.L.R. Thomas.)

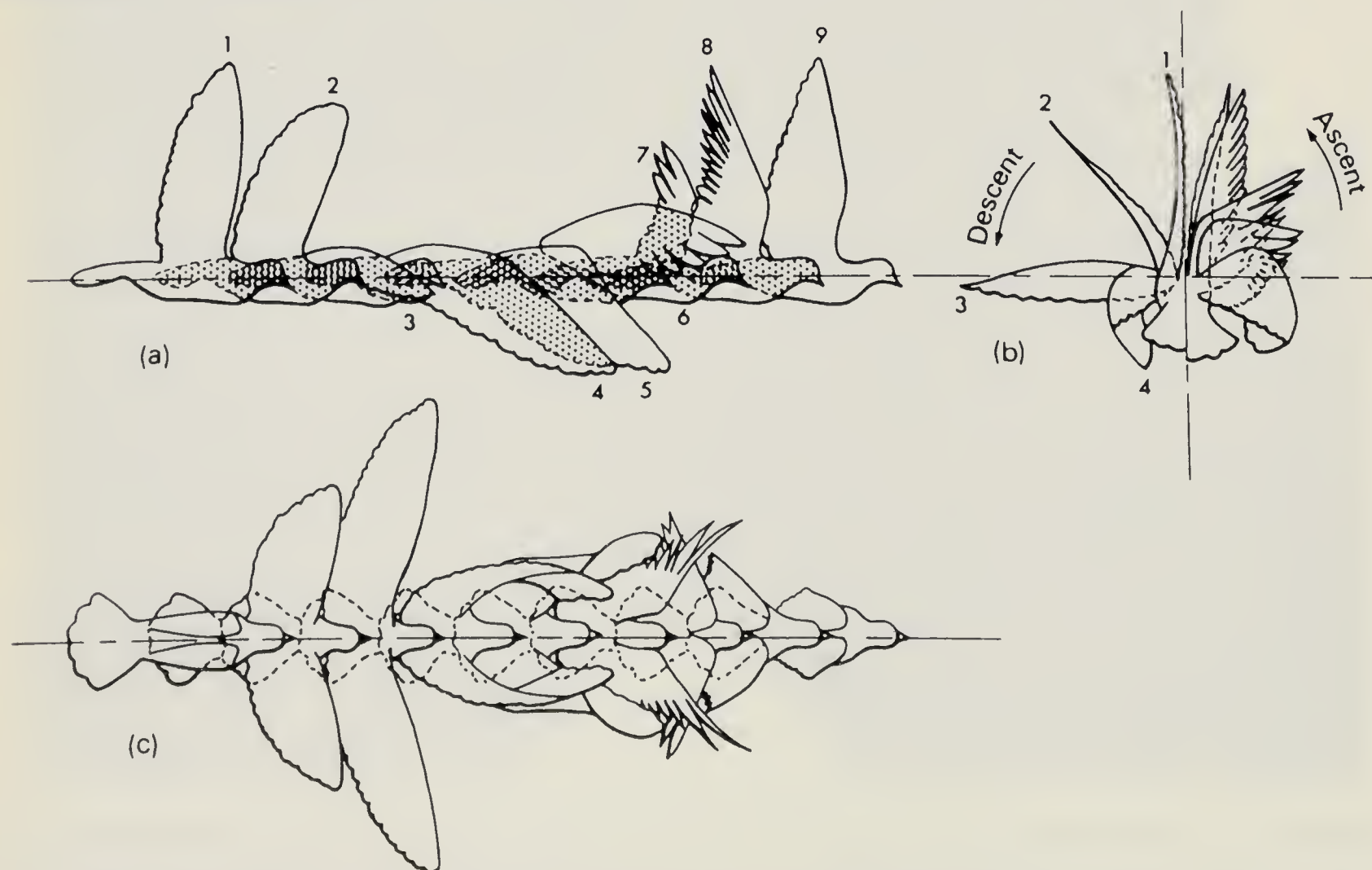


FIGURE 5a – Wingbeat kinematics. Pigeon *Columba livia* in very slow flight. (From Guidi 1939.)

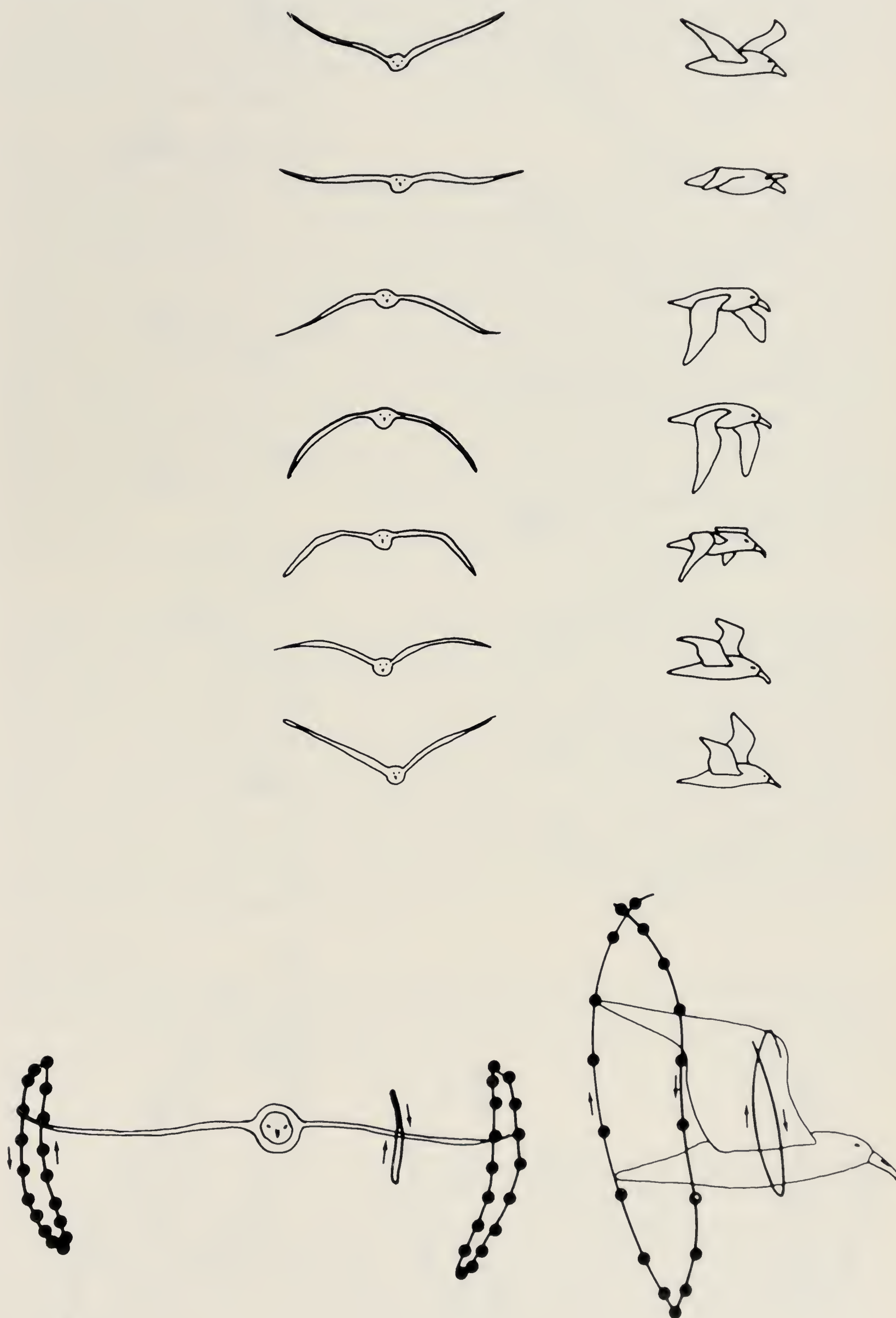


FIGURE 5b – Cruising flight in Black-browed Albatross *Diomedea melanophris*. (From Scholey 1983.)

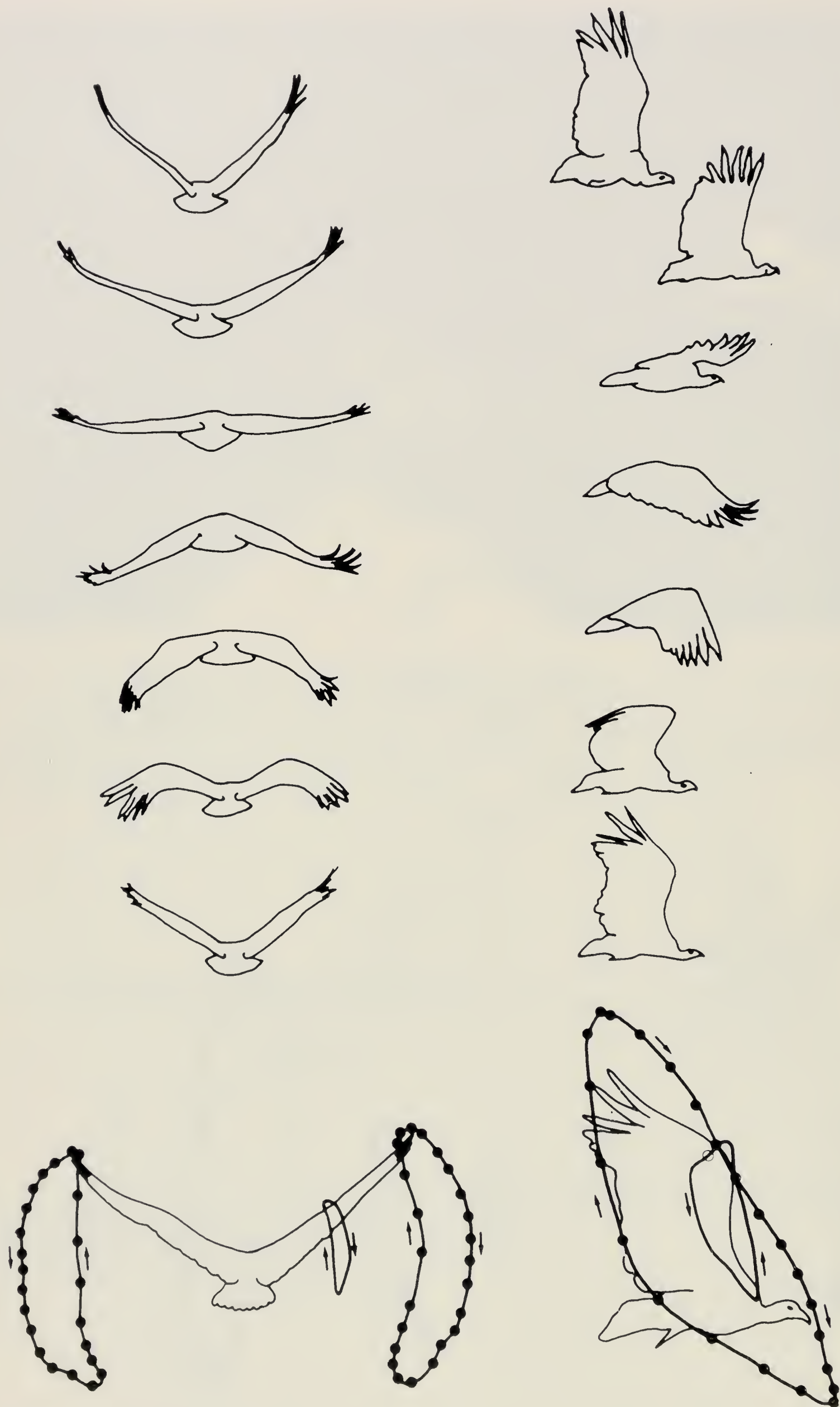


FIGURE 5c – Cruising flight in Ruppell's Griffon Vulture *Gyps ruppellii*. (From Scholey 1982.)

This *vortex ring* gait with an inactive and highly flexed upstroke is typical of slow flight in many birds, and is similar to the gait generally adopted in hovering (except by hummingbirds). It is also used by many small passeriforms (especially in bounding flight), and is widespread in galliforms, rails and other species with short, rounded wings, regardless of flight speed.

The continuous wake gait

In longer-winged birds, it becomes possible at higher speeds to use the upstroke to generate lift (Figure 5b). This gait is associated with the continuous vortex wake, and is characteristic of many birds in cruising or fast flight, particularly species with high aspect ratio and pointed wings, including pigeons, falcons, ducks, gulls, petrels (Scholey 1983). As in all gaits the wing is outstretched and planar during the downstroke; during the upstroke it remains nearly flat, but is flexed at the carpal joint and the wingtip is swept back so that wingspan is reduced (Scholey 1983, Rayner 1986, 1988a). Birds flying with this gait can be identified by three factors: the stroke plane is perpendicular to the axis of flight, the upstroke and downstroke are equal in duration, and when seen laterally the track of the wingtip is an ellipse. This gait is simple and efficient, and anatomically straightforward; a mathematical model is discussed below. I consider it of considerable phylogenetic importance, as it is probably the primitive gait used by the first birds to evolve flight (Rayner 1988b); this is supported by its close relationship with the line vortex wake in gliding.

A slightly different gait is found in birds with lower aspect ratio, most commonly in species with low wing loading and square wings, and frequently with separated primary feathers (Figure 5c), in particular owls, raptors, herons, cranes, storks and some Pelecaniformes. Again, the wing is fully extended in the downstroke, but wingbeat amplitude is greater, the upstroke is shorter than the downstroke, and the stroke plane is tilted. In the upstroke the arm wing is flexed, and the track of the elbow is highly elliptic. In owls the vortex wake associated with this gait is vortex rings (Figure 3), and the upstroke is passive. I am uncertain whether this is the case in larger birds using this gait, although analysis of film of both Old- and New-World vultures suggests a significant downward deceleration during the upstroke corresponding to the absence of weight support during that phase.

Gait selection

Most birds change gait as speed increases, with a tendency in longer-winged species to adopt a lifting upstroke so that force equilibrium can be maintained although the components of drag vary independently. The conditions under which gait should change are not yet fully understood, and a number of important questions must be raised:

- (1) Is it right to assume that birds can select speed freely, or are some species designed for a narrow range of speeds suited to their ecology? I have shown that pigeons have difficulty flying at low speeds even with the vortex ring gait, and may not be able fully to support their weight, and this slow speed gait may be confined to accelerated flights.
- (2) When is it better to use the upstroke to help support the weight, despite the negative thrust, and when should it be passive and all lift be concentrated on the downstroke?
- (3) At what speed should the gait change, and is this speed specific to any bird?
- (4) Does the selection of gait depend on flight morphology?

In terms of mechanical and aerodynamic efficiency the optimum gait is the continuous vortex wake. This gait can only work if the bird can maintain constant circulation with a shortened wing during the upstroke; this is not possible with short wings (hence high wingbeat frequency) or in slow flight because local angles of incidence are too great. In such circumstances the best alternative is to dispense with force generation from the upstroke, and instead to flex the wing to minimize profile drag and inertia. The result is the vortex ring gait. Thus gait is determined by both morphology and flight speed, and this is in agreement with our observations from flow visualization and high-speed photography.

ESTIMATION OF FLAPPING FLIGHT ENERGETICS

Energy is a major demand for flying birds, and its quantification is essential if we are to understand the importance of flight in a bird's biology. There are two approaches to this problem: power in flight can be measured directly through gas exchange or water metabolism, or theoretical models may be derived from which mechanical power (and hence indirectly metabolic power) may be estimated (e.g. Rayner 1986, 1988a, 1990).

Theoretical models of flapping flight

In the last century many theories were aimed at the construction of ornithopters, and their conspicuous lack of success resulted from misunderstanding of the mechanics of aerofoil action, and from concentration on the need to generate weight support - rather than thrust - by flapping. The first reasonably realistic model of flapping flight was that of Gnosspelius (1925), based on steady-state 'blade element' theory; this was the first to demonstrate that mechanical power in birds - as in aircraft - follows a U-shaped curve against flight speed. Like all later blade-element and related models (e.g. Pennycuick 1968) it suffers from the deficiency that aerofoil characteristics in flapping flight vary during the wingbeat, and probably differ substantially from those measured in gliding. A pragmatic model developed by Pennycuick (1969, 1975), and later reformulated by Tucker (1973) and Greenewalt (1975), is loosely based on the steady lifting line theory, central to fixed aerofoil aerodynamics. This incorporates the effects of bound and wake vorticity, but models lift for a fixed wing only and therefore neglects the energy cost of generating thrust, which is the central feature of flapping flight. Although they give little insight into flapping flight aerodynamics, these models are simple to use, and since weight is the dominant force on a flying bird, give reasonable estimates of total power in flight.

I have argued above that the vortex wake is central to force generation in flight. As we now know the wake structure from flow visualization, it is feasible to develop realistic aerodynamic models of flapping flight, from which various mechanical quantities associated with flight may be estimated. A passive upstroke leads to a vortex ring wake, and I developed a time-averaged unsteady lifting-line model to predict total mechanical power (Rayner 1979, 1980). This model predicted that to minimize power, a bird should adjust wingbeat kinematics with flight speed, and that the upstroke should become active at intermediate speeds (but modelling that situation was beyond the capacity of the vortex ring theory). The discovery that in faster flight circulation is constant - and therefore the absence of the complications of transverse vorticity - is the foundation of a model of the continuous wake gait (Rayner 1986, 1987, 1988a,

1990) which is also based on unsteady lifting line theory. Full account is taken of wingbeat kinematics, which are predicted under conditions of force equilibrium and energy minimization.

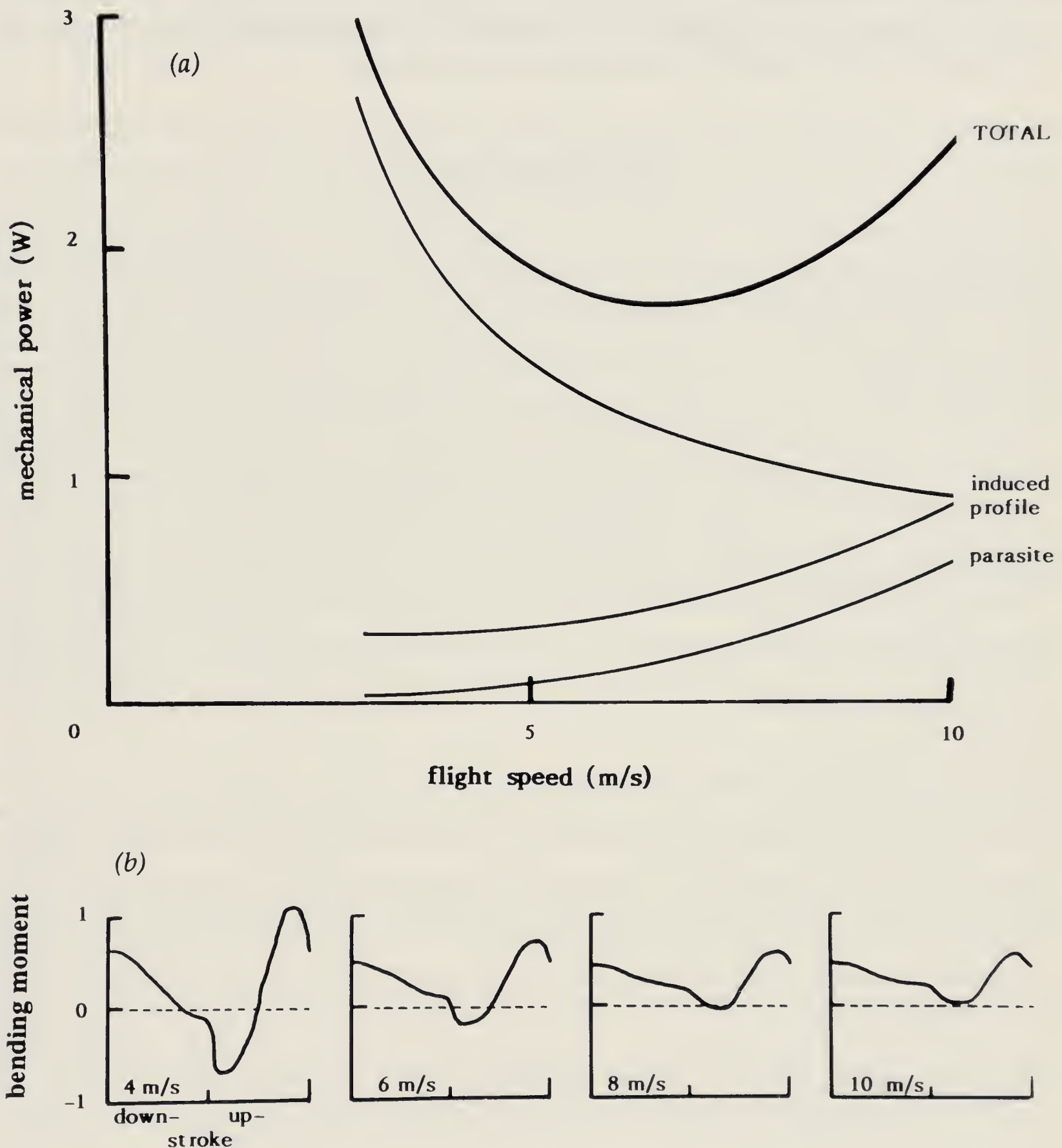


FIGURE 6 - Estimated flight performance of the Kestrel *Falco tinnunculus* with active upstroke and constant circulation, and continuous vortex wake. For full details see Rayner (1988a). (a) Variation of components of mechanical power with flight speed. (b) Time course of total wingroot roll moments at different flight speeds, including components due to lift, induced drag, profile drag (very small), wing mass and wing inertia; no net work is done against inertia. Peak moment invariably occurs in the latter part of the upstroke. At higher speeds the moment is always positive, indicating that no muscular effort is required to elevate the wing. At lower speeds the moment is negative in the early phases of the downstroke, and the supracoracoideus should become active to elevate the wing.

A typical curve of mechanical power against velocity is shown in Figure 6a. The rise in induced power at high speeds is caused by the change in wingbeat kinematics

needed to maintain thrust as parasite and profile drags increase; this feature was ignored in previous models (e.g. Pennycuick 1968). Predicted circulation and kinematics agree closely with those measured in several animals. Kinematics should change with flight speed, with frequency and amplitude falling as speed increases. At low speeds it is advantageous for the upstroke to be aerodynamically inactive, the animal must change gait, and the vortex-ring model is more realistic.

Estimation of wingroot roll moments at the humeral joint (Figure 6b) generates a number of predictions which may be tested experimentally by methods of Dial et al. (1988). The roll moments are those exerted by the wing on the (rigid) body, and are proportional to the force exerted by the pectoral muscles (pectoralis and supracoracoideus) as they depress and elevate the wing. A positive moment corresponds to a downwards force from the pectoralis, and a negative moment indicates that the supracoracoideus is generating force. Muscle force is not in phase with lift because the dominant force for much of the wing stroke is inertia. At medium and high flight speeds, the moment never falls below zero, and aerodynamic lift is more than sufficient to elevate the wing: the supracoracoideus is not needed and the pectoralis should be active throughout the wingbeat (although the number, and perhaps the type, of active muscle fibres probably varies). At lower speeds the moment is negative during the latter part of the downstroke, and the abductor muscles should begin activity in the mid-downstroke rather than simply contracting during the upstroke. At all speeds peak depressor activity occurs during the final half of the upstroke. Tentative confirmation of these predictions comes from electrophysiological recordings of muscle activity in birds and bats flying at different speeds (Dial et al. 1988; see also Rayner 1986, 1987).

Metabolic power and flight efficiency

However accurate they may be as descriptions of flight mechanics, all mechanical power models have a serious limitation. They estimate the rate of increase of kinetic energy in to the surrounding air. This quantity may be equated with power output from the flight muscles, but its relation to metabolic energy in flight is tenuous; total energy consumption is presumably the greatest influence on the bird's decision making. Tucker (1973), Greenewalt (1975) and Pennycuick (1975) all assumed - with no experimental justification - that mechanical and metabolic powers are directly proportional, and that muscle efficiency is constant (of the order of 20-25%). Efficiency is sensitive to a wide range of factors, and comparison of mechanical estimate and metabolic measurement suggests it should increase sharply as mass to the power $1/4$, as in terrestrial mammals, and for most smaller birds is appreciably lower than the empirical value of 0.25 (Rayner 1990). Moreover, wing root forces and wingbeat kinematics vary, and efficiency is unlikely to be independent of speed and gait. Far too little is currently known of the thermal physiology of bird flight muscles to explore this with any confidence, and existing estimates of efficiency may be inaccurate. These limitations probably provide at least a partial explanation for the widely reported discrepancy between predicted and measured metabolic power consumption in some birds (Rayner 1986, 1990). There is currently no reason to doubt either metabolic measurements or the more firmly grounded mechanical predictions of power, but energy and performance criteria predicted on mechanical grounds may have only indirect significance for the true energy demands experienced by the animal (Rayner 1990). The reconciliation of these disparate physical quantities remains the major challenge for the future study of avian flight performance.

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NEUROMUSCULAR ORGANIZATION FOR FLIGHT: ISSUES FOR STUDY

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ABSTRACT. The pectoralis, the major depressor muscle of the wing, is structurally and functionally complex but its neuromuscular organization for flight remains relatively unexplored. We have begun a series of investigations at the motor unit level in two species with contrasting flight styles, the Domestic Pigeon *Columba livia* and the European Starling *Sturnus vulgaris*. Thirty motor units from the pectoralis of anaesthetised Domestic Pigeons have been isolated. Of these units, 29 were relatively small and one relatively large. When tested for fatigue resistance, 75% of the units were resistant and 25% fatigable. These data are consistent with the hypothesis that within the pectoralis of Domestic Pigeons, two populations of motor units exist which are functionally partitioned for function.
Keywords: Flight control, motor units, recruitment.

INTRODUCTION

Several years ago while reviewing some high speed films of raptors attacking and striking their prey, I recall my wonder at a Goshawk's ability to alter so quickly and with such grace its entire body orientation in space within a single wingbeat. This split-second precision requires a complex interplay of the sensory and motor components of the flight apparatus. Along with several colleagues and students, I am involved in a series of studies designed to address the neuromuscular organisation of the muscles responsible for wing movements in two species of birds, the Domestic Pigeon *Columba livia* and the European Starling *Sturnus vulgaris*. These two species differ in their flight characteristics which may help us to delineate features specific to each as well as those that are general for flight. This is an exciting time for studies of animal flight. Technological advances are enabling scientists to test a number of hypotheses regarding muscle function and efficiency which bear not only on the evolution of different flight styles and morphologies, but even the evolution of flight in fossil forms (Rayner 1989, Ruben 1990). We employ a number of experimental techniques to better understand wing kinematics during flight as well as the mechanics of the muscles which underlie movements seen. This summary will focus on some of our ongoing studies of the organization of the motor units for use in the primary depressor muscle, the pectoralis.

Recent studies reveal that the pectoralis of birds is surprisingly complex. Studies of anatomically complex muscles producing jaw and limb movements in reptiles and mammals illustrate a correlation between peripheral neuromuscular organisation and function (Herring et al. 1979, Weijs & Dantuma 1981, English & Weeks 1987). Individual branches of muscle nerves may innervate discrete groupings of muscle fibres within a gross muscle to provide a neuromuscular compartment which, in turn, may be organised to perform a specific behavioural task. Although aspects of this concept are controversial (Windhorst et al. 1990), it provides a useful framework from which

to begin this paper and for discussing the general functional organisation of the pectoralis.

GENERAL ORGANIZATION OF THE PECTORALIS

In many birds (including Pigeons and European Starlings) the major part of the pectoralis (pars pectoralis) is divided by a sheet of connective tissue into two heads, the sternobrachialis (SB) and thoracobrachialis (TB) (Simic & Andrejevic 1963, Vanden Berge 1979). Although both heads insert onto the deltopectoral crest of the humerus, they possess separate origins and fibre orientations and apparently are innervated by distinct nerve branches from the brachial plexus (Kaplan & Goslow 1989). Stimulation of these two nerve branches in Pigeons reveals that the SB is capable of humeral depression as well as protraction and the TB of depression as well as retraction (Dial et al. 1988). Anatomical tracer studies of the neurons innervating the SB and TB of Pigeons also illustrates an organisation within the spinal cord suggestive of a functional differentiation in their use (Sokoloff et al. 1989). As might be anticipated, electromyograms (EMGs) of the SB and TB from free-flying Pigeons (Dial et al. 1987, 1988) and Starlings (Dial et al. 1991) support a hypothesis that the SB and TB are used differentially during different flight modes.

A functional partitioning of the pectoralis has broad implications for the neural control of flight and serves as a springboard for subsequent studies. There are data for both Pigeons and Starlings which suggest that within the SB and TB, further functional specialization exists at the motor unit level. A brief review of motor unit organisation and use is in order.

MOTOR UNIT ORGANIZATION AND FUNCTION

A motor unit, the smallest functional unit of neuromuscular organisation, consists of a single neural component, the motoneuron, and the collection of muscle fibres it innervates, the muscle unit. Within the ventral horn of the gray matter of the spinal cord, the cell bodies of motoneurons that send axons to a particular muscle are clustered in motor pools. Within a muscle's pool, or across pools for groups of muscles, motoneurons are thought to be selectively activated to complete a locomotor task (for review, Burke 1981, Stuart & Enoka 1983, English 1985). Following the all-important series of papers by Elwood Henneman in the mid-1960's, studies of the anatomical and physiological properties of isolated motor units have substantially enhanced our understanding of the neuromuscular basis for locomotion. The formulation of an order of motoneuron recruitment based upon the size principle (Henneman & Mendell 1981, Binder & Mendell 1990) has provided a conceptual framework for motor unit organisation which is testable and may now be extended to birds (but see Zajac 1990).

The SB and TB of the Pigeon are comprised of two distinct populations of muscle fibre types (Figure 1): large fibres (78.2 μm diameter), which appear to have little aerobic capacity (based on histochemistry) and small fibres (33.5 μm diameter), which appear to be richly aerobic (George & Naik 1960, Talesara & Goldspink 1978, Kaplan & Goslow 1989). The electromyographic studies of Dial et al. (1987, 1988) suggest

that the large, anaerobic fibres in the Pigeon are used preferentially for takeoff and landing but not for level flight whereas the small, aerobic fibres are used for all modes of flight. The histochemical organisation of the pectoralis of the European Starling differs in several respects from that of the Pigeon. In contrast to the bimodal population of fibre size and aerobic capacity found in the pectoralis of the Pigeon, this muscle of European Starlings consists entirely of small, aerobic fibres (Rosser & George, 1986). It should be noted, however, that based on differences in aerobic histochemistry, these authors recognise two types of fibres in the Starling pectoralis.

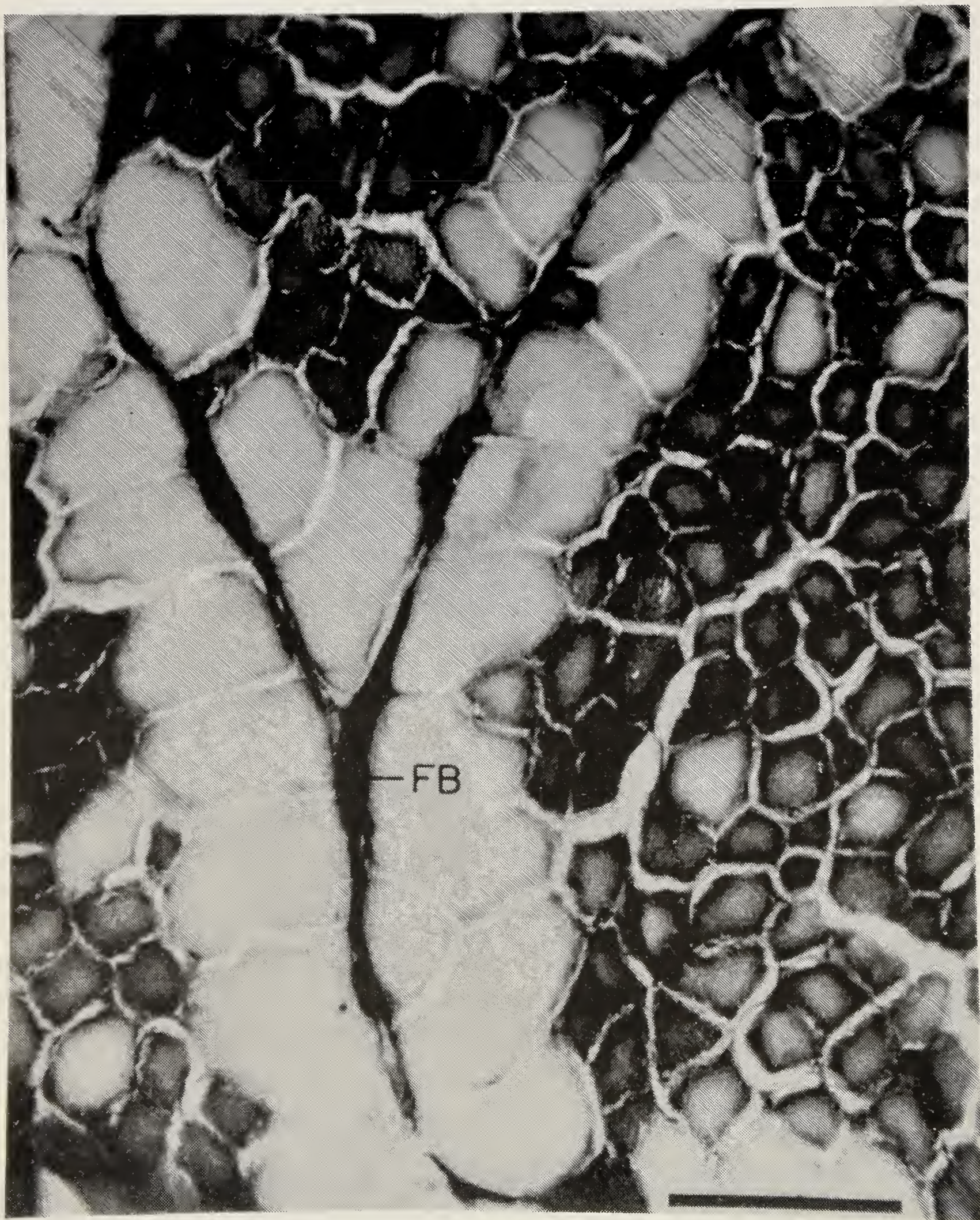


FIGURE 1 - Large and small fibres in the pectoralis of *Columba livia*. Photomicrograph is a frozen section (20 μm) from the SB, stained for myofibrillar ATPase after acid preincubation (pH 4.35). Two populations of fibres are evident. FB - fascicle boundary. Scale bar equals 200 μm . After Dial et al. (1987).

Among flying animals, it seems likely that selection must act to optimize overall mechanical and chemical performance of the muscles that drive the wing while maintaining plasticity in the locomotor system. Fundamental constraints of contractile protein design dictate the existence of a narrow range of contraction speeds for maximum efficiency (Goldspink 1977, 1981); thus, flight muscles in birds might be designed to operate at a fixed level of power output which allows for predictions of fiber recruitment. Several studies have addressed fibre recruitment in bird flight muscle based on empirical data or theoretical considerations. Gulls *Larus argentatus*, like Pigeons, possess two distinctly different sized muscle fibres in the pectoralis. In their study of gulls flying and gliding in a wind tunnel, Goldspink et al. (1978) noted amplitude changes in the EMGs and speculated about motor unit recruitment order, but as in the studies of Dial et al. (1987, 1988) their interpretation was limited by a lack of knowledge concerning motor unit organisation and contractile properties.

In a thoughtful paper, Rayner (1985) draws conclusions about the recruitment of muscle fibres in two groups of birds which characteristically fly with intermittent periods of ballistic or gliding flight. He notes that in some of these species (European Starlings included), the pectoralis is comprised of a relatively homogeneous population of aerobic fibres and that wingbeat frequency and amplitude remain relatively constant over a range of flight speeds. Rayner deduced that muscle contraction dynamics remain near optimum and, accordingly, all (or virtually all) aerobic fibres within the pectoralis might be expected to be recruited with each downstroke. Clearly, some knowledge of the neuroanatomical and neurophysiological properties of the motor units which comprise the pectoralis of Pigeons and Starlings is needed in order to better evaluate these fundamental questions regarding motor unit use.

MOTOR UNIT STUDIES IN *COLUMBA LIVIA*

Welsford et al. (1991) have initiated studies of isolated motor units from the pectoralis muscle of Domestic Pigeons to determine the functional correlation to the two types of muscle fibres noted as well as to gain some understanding of their contractile properties as related to flight. Motoneurons were isolated intracellularly or extracellularly in adult, anaesthetised birds. Of the 30 units isolated from the SB, 29 units were small and generated 0.22% or less of the maximum tetanic tension of the entire SB. One exceptionally large unit developed a peak tension of 0.56% whole muscle tension (Figure 2). When tested for fatigue resistance, 75% of the units were considered resistant and 25% fatigable (Figure 3).

The expectation (based on studies in mammals) is that during takeoff and landing, when airspeed is low and high power output necessary, populations of units capable of producing large forces will be recruited. It is anticipated that within the Pigeon pectoralis, two distinct populations of motor units will be seen relative to size and fatigability. These limited data support such a hypothesis. The units comprising the Starling pectoralis, in contrast, might be expected to fall within a continuum for these two parameters. An investigation of the units in this species remains to be done. Clearly, larger samples of units are needed before conclusions can be formulated with confidence. We believe, however, that studies such as these will yield data for our understanding of not only the neural control of flight, but of the evolution of this remarkable mode of locomotion.

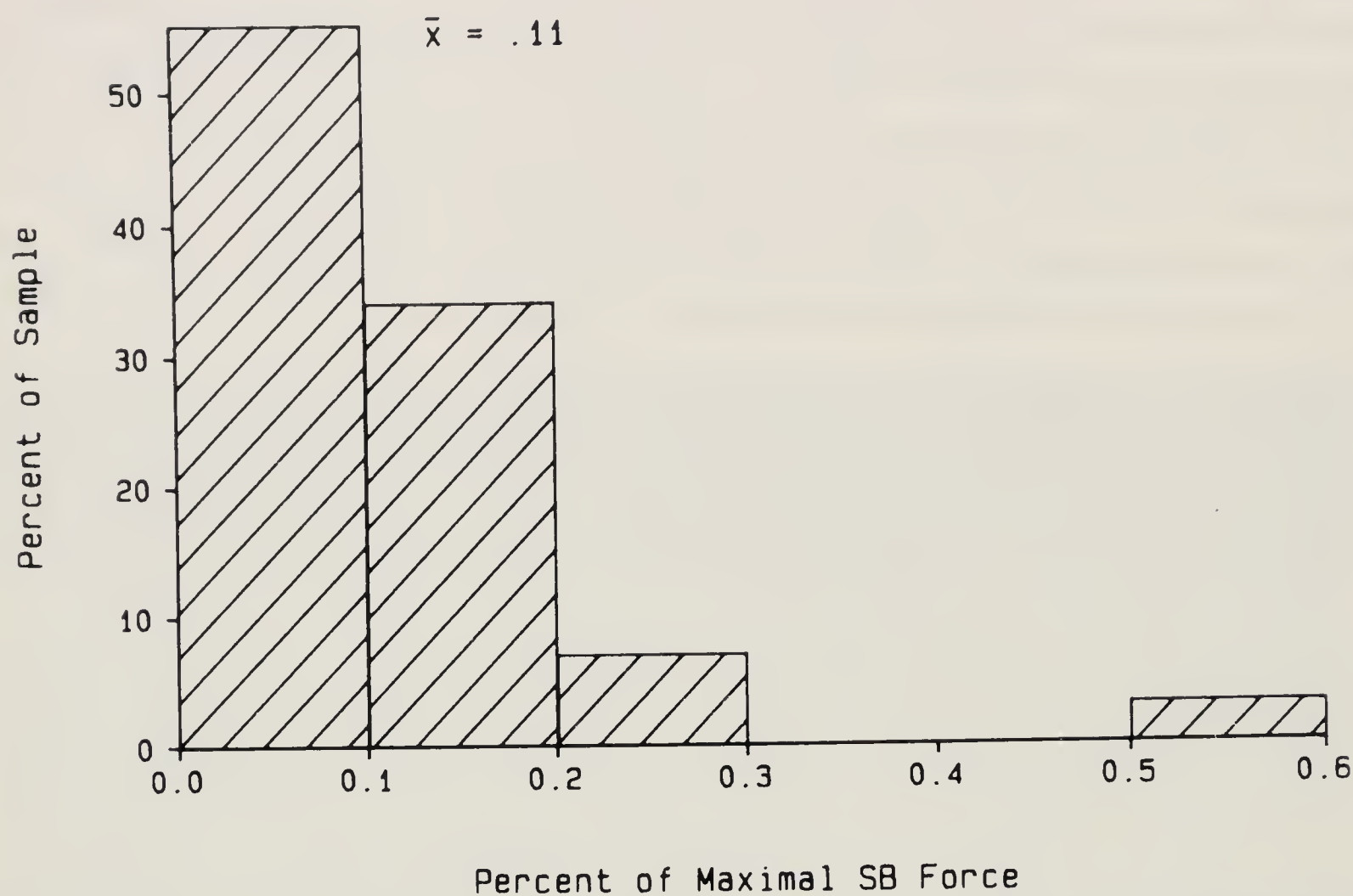


FIGURE 2 - Distribution of maximal tetanic tensions of SB muscle units expressed as a percentage of SB tetanic force. Mean = 0.11% (n = 30). After Welsford et al. (1991).

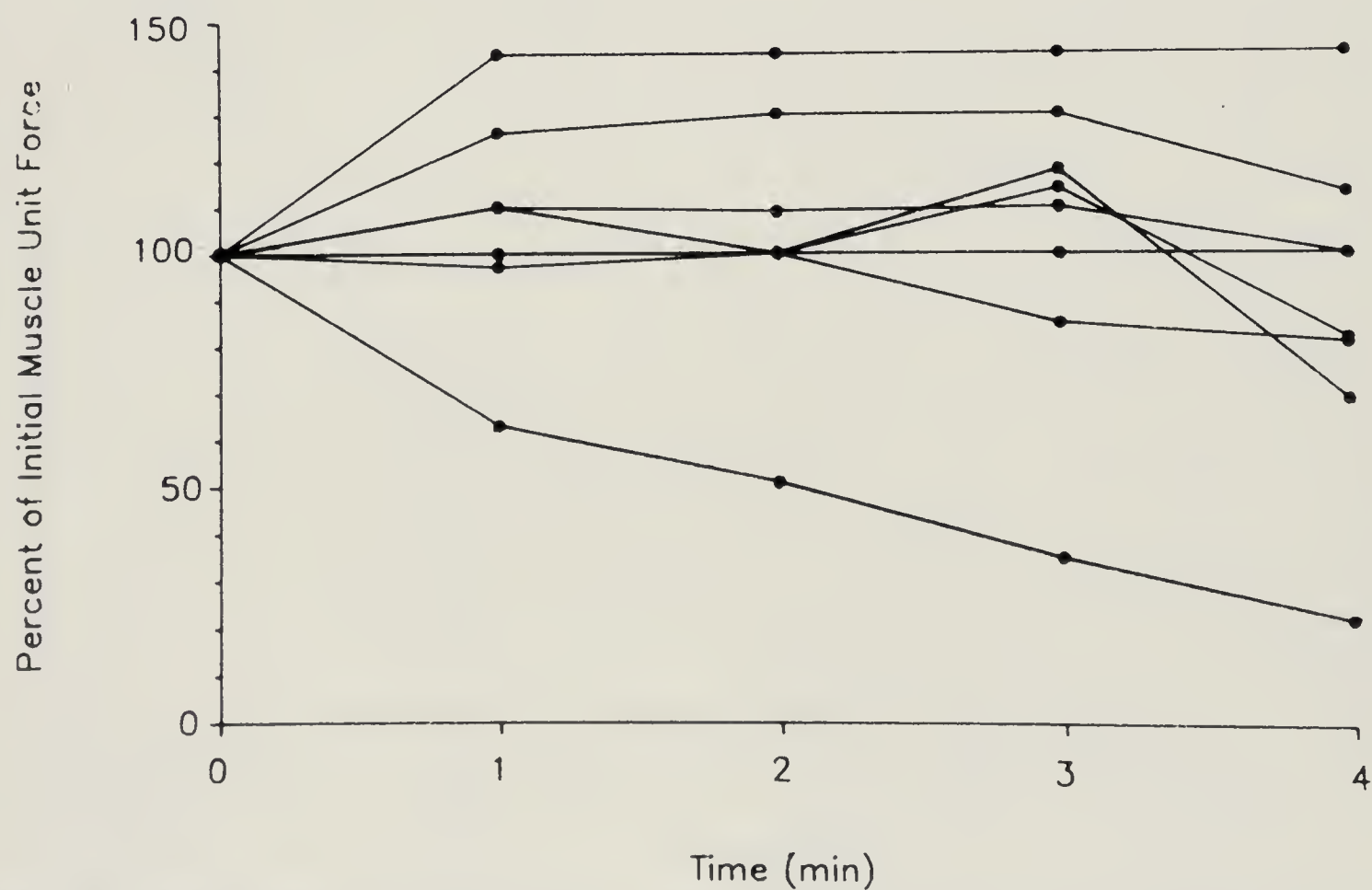


FIGURE 3 - Fatigability of SB muscle units during four minutes of stimulation (500 msec of each second) at 60 Hz, expressed as percent of initial muscle unit force (n = 9 from two experiments). After Welsford et al. (1991).

ACKNOWLEDGMENTS

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CORE TEMPERATURE RELATIONS OF PIGEONS DURING PROLONGED WIND TUNNEL FLIGHT

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ABSTRACT. Using thermistors, core temperature T_c was measured in pigeons *Columba livia*, (breed "Grippler") during rest and during flight in a wind tunnel. Mean T_c at rest was $39.8 \pm 0.7^\circ\text{C}$ and was independent of ambient temperature T_a ($10\text{-}30^\circ\text{C}$). In the first minutes of flight, T_c increased to $1.5\text{-}3.0^\circ\text{C}$ above resting level and remained at this higher level. This hyperthermia increased with T_a ($v = \text{const.}$). It was more or less constant in the low T_a range ($10.6\text{-}13.9^\circ\text{C}$) at flight speeds v ranging from 10 to 18 ms^{-1} and normal body mass, but increased with v and elevated body mass in the high T_a range ($23.7\text{-}28.8^\circ\text{C}$). Flight behaviour with and without instrumentation was essentially the same. Hyperthermia during flight was lower in our well trained long flying (more than 3 hrs in the wind tunnel) pigeons than in short flying birds used by other authors, but present in all flights analyzed. The meaning of hyperthermia is discussed.

Keywords: Pigeon, *Columba livia*, temperature, core temperature, wind tunnel flight, flight behaviour.

INTRODUCTION

The metabolic rate of a bird during flight is at least ten times higher than during resting. Taking into consideration that approximately 25% of the metabolic rate is required for muscle activity, the remaining 75% which is transformed into heat must be disposed of should the bird not become overheated during long flights.

According to results obtained in wind tunnel tests (Rothe, Biesel & Nachtigall 1987) the relative metabolic rate of a "Grippler" Pigeon *Columba livia* of average mass (mean body mass 0.33 kg) was calculated to be 68 W kg^{-1} for free flight in nature. This gives an absolute metabolic rate of approximately 24 W from which 6 W are required for flight performance and 18 W must be discharged as heat.

Several areas on the body, wings and extremities are available for discharging surplus heat (Figure 2a). Heat dissipation is favoured by especially high body temperatures which may be higher than under resting conditions (hyperthermia). The questions arose, which values of hyperthermia are used by the flying animals and what are the internal and external limiting conditions for hyperthermal constancy during long distance flights (which in turn indicate unproblematic heat loss).

METHODS

Wind tunnel and animals

A special wind tunnel was developed and built for these tests (Figure 1a) and a series of well trained pigeons belonging to the "Grippler" race (Figure 1b) was used. Details are to be found in Rothe and Nachtigall (1987).

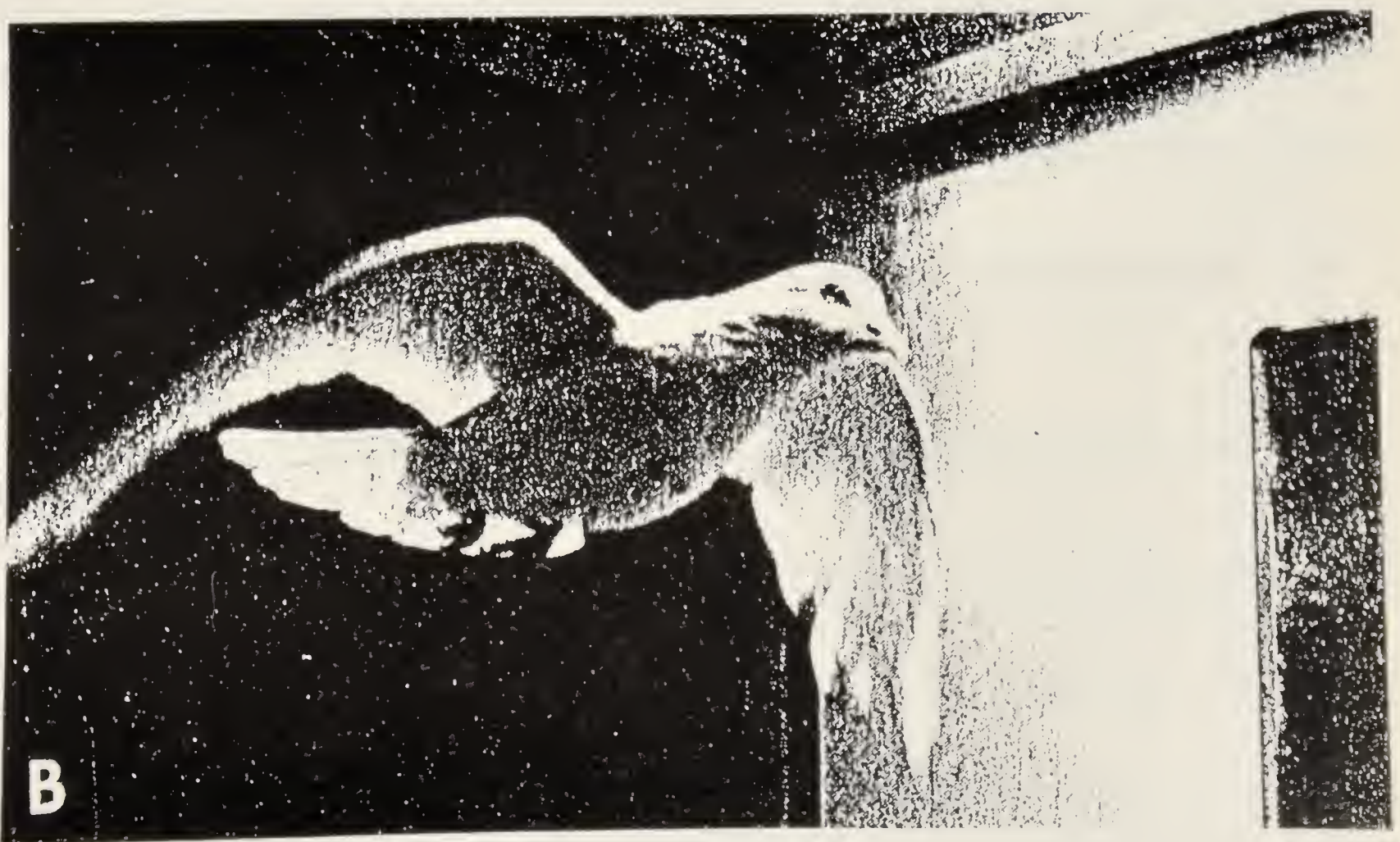
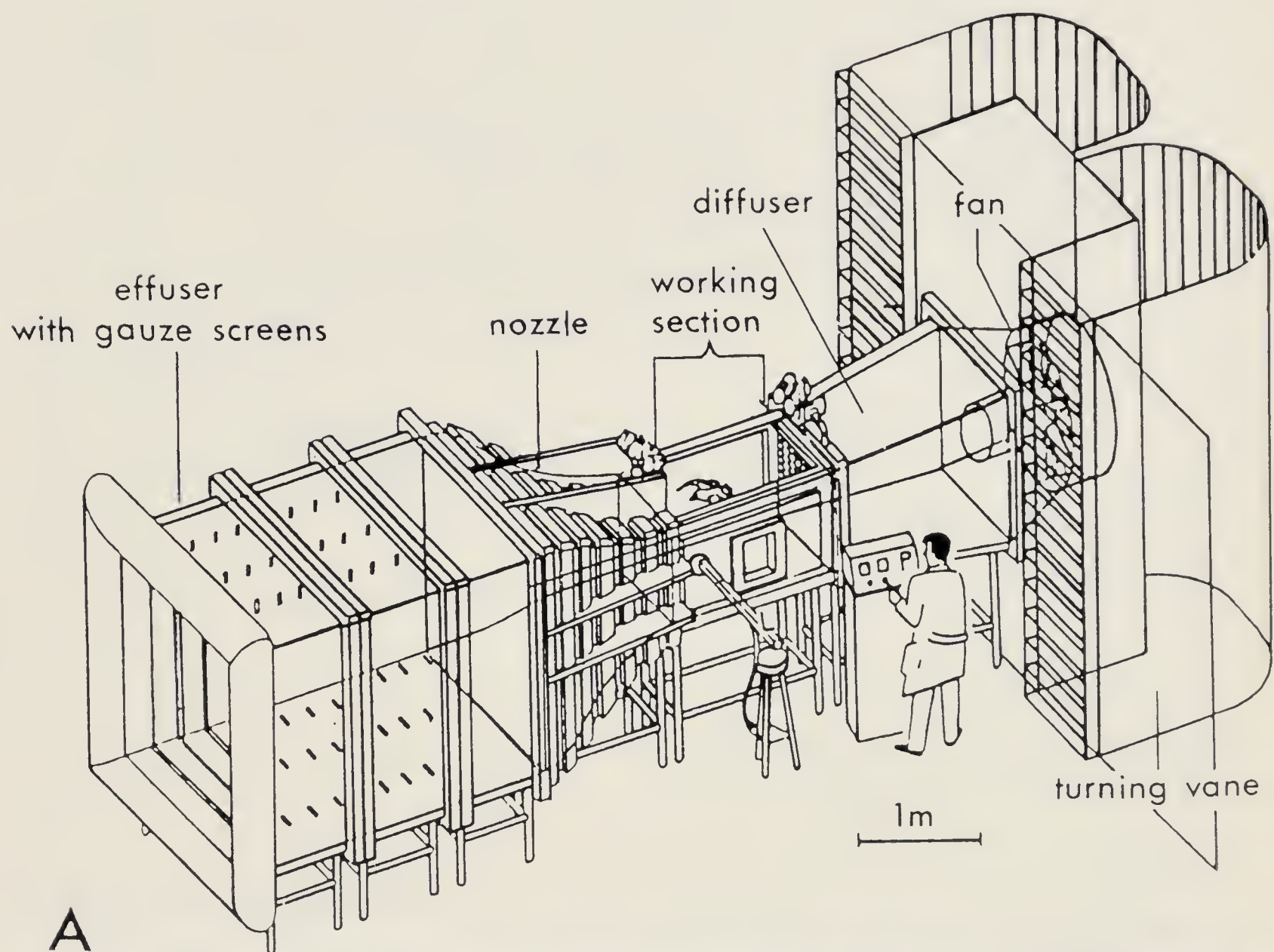


FIGURE 1 - Pigeon flight in a wind tunnel. (A) Large wind tunnel used by the Arbeitsgruppe Nachtigall at the Institute of Zoology, University of Saarland, and built for the analysis of bird flight. (B) Pigeon flying in the measuring area of the wind tunnel.

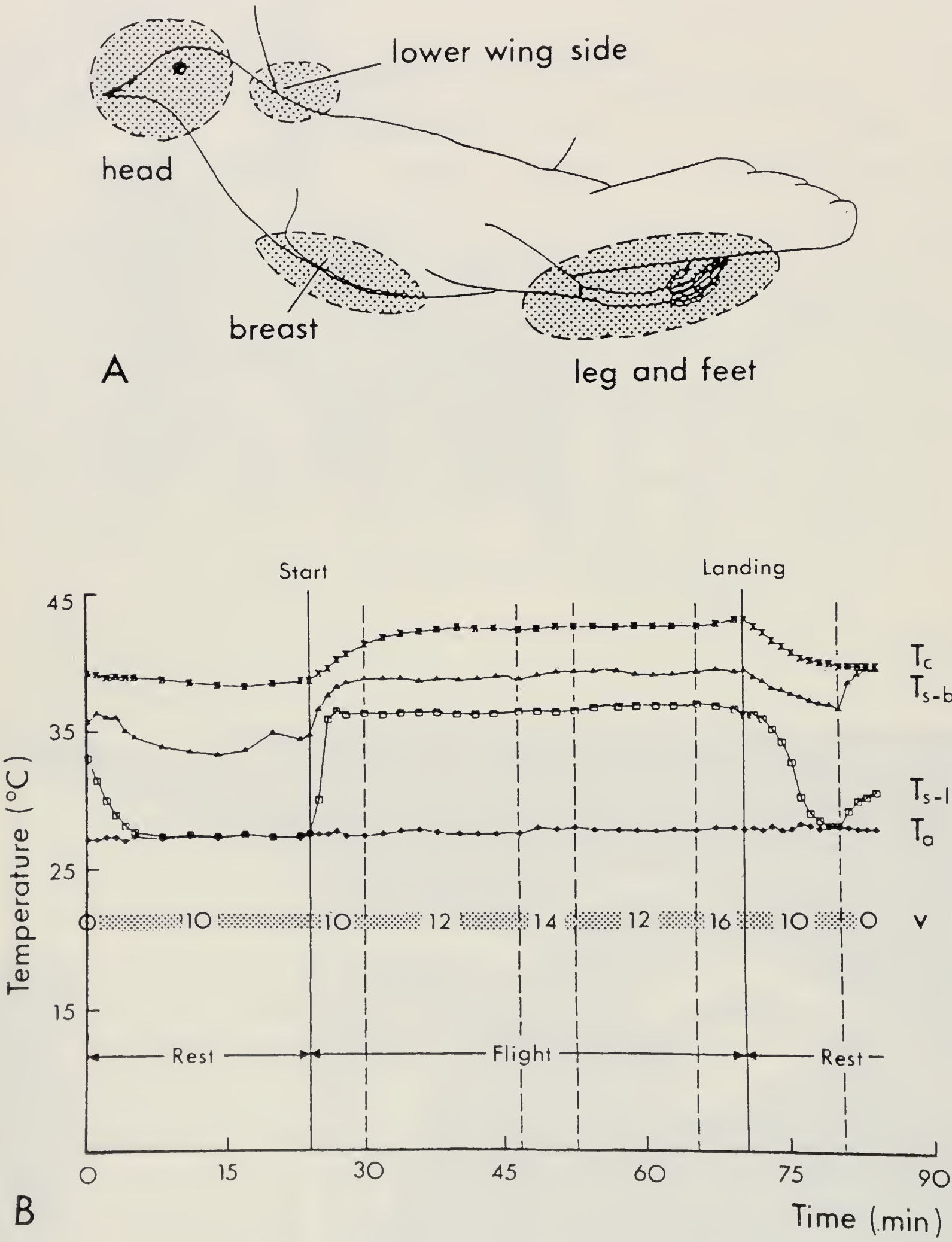
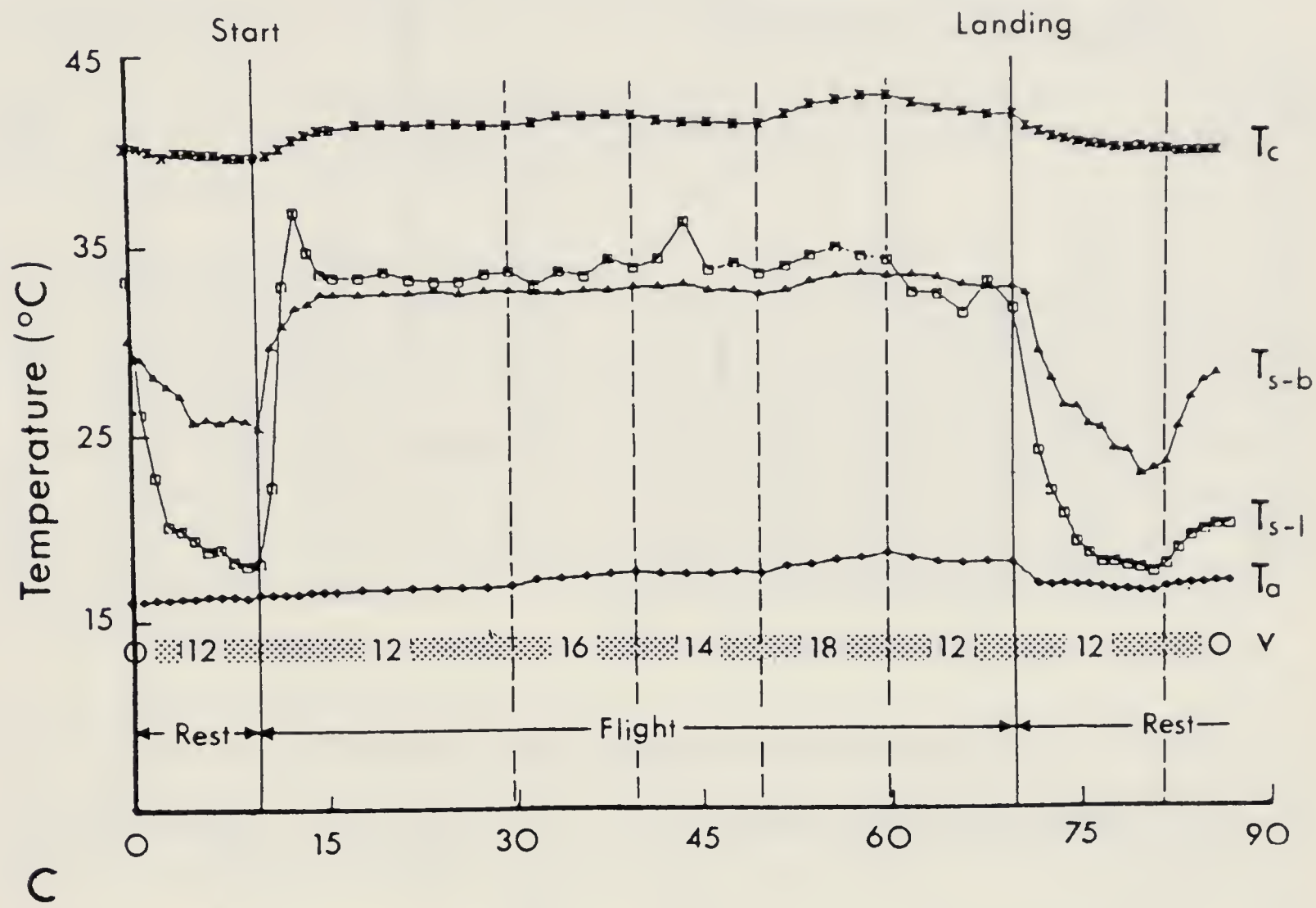


FIGURE 2 - Temperature relationship in flying Grippler pigeons. (A) Heat loss areas (dotted areas) and measurement of core temperature T_c . (B) Changes in core temperature T_c and ambient temperature T_a at rest and at different speeds v during a long flight. Speed was altered step-wise. High ambient temperature. (C) like B, lower ambient temperature.

FIGURES 2 – Continued.



Temperature measurements

In order to measure the core temperature of the body a Siemens M 85 thermistor ($\pm 0.1^\circ\text{C}$) was placed deep in the colon. An extremely fine, flexible conducting wire led from the sealed cloaca to a central registering unit which also measured the temperature of other areas of the body (not discussed here; see Hirth, Biesel & Nachtigall 1987) in short intervals via a multiplexer. The extra mass of 4 g coming from the measuring system was only 1% of the body mass and did not cause any recognisable anomalies in behaviour.

The whole wind tunnel room could be heated or cooled to change the environmental temperatures.

Experimental procedure

Before beginning with an experiment, the test bird was weighed, the thermistor put in place and the bird was then set on a perch within the test area of the wind tunnel under low light intensity. The core temperature of the bird sitting without wind, sitting with the wind (speed $10\text{--}12\text{ ms}^{-1}$) turned on and flying at different wind speeds was measured until a constant temperature was obtained in each situation. The experiment usually lasted 30 minutes, during which time the flight speed was altered several times. Immediately after flight was stopped, the resting temperature value was measured again with and without wind in reverse order.

RESULTS

Flight behaviour

The pigeons demonstrated typical flight behaviour, i.e. beating phase punctuated with

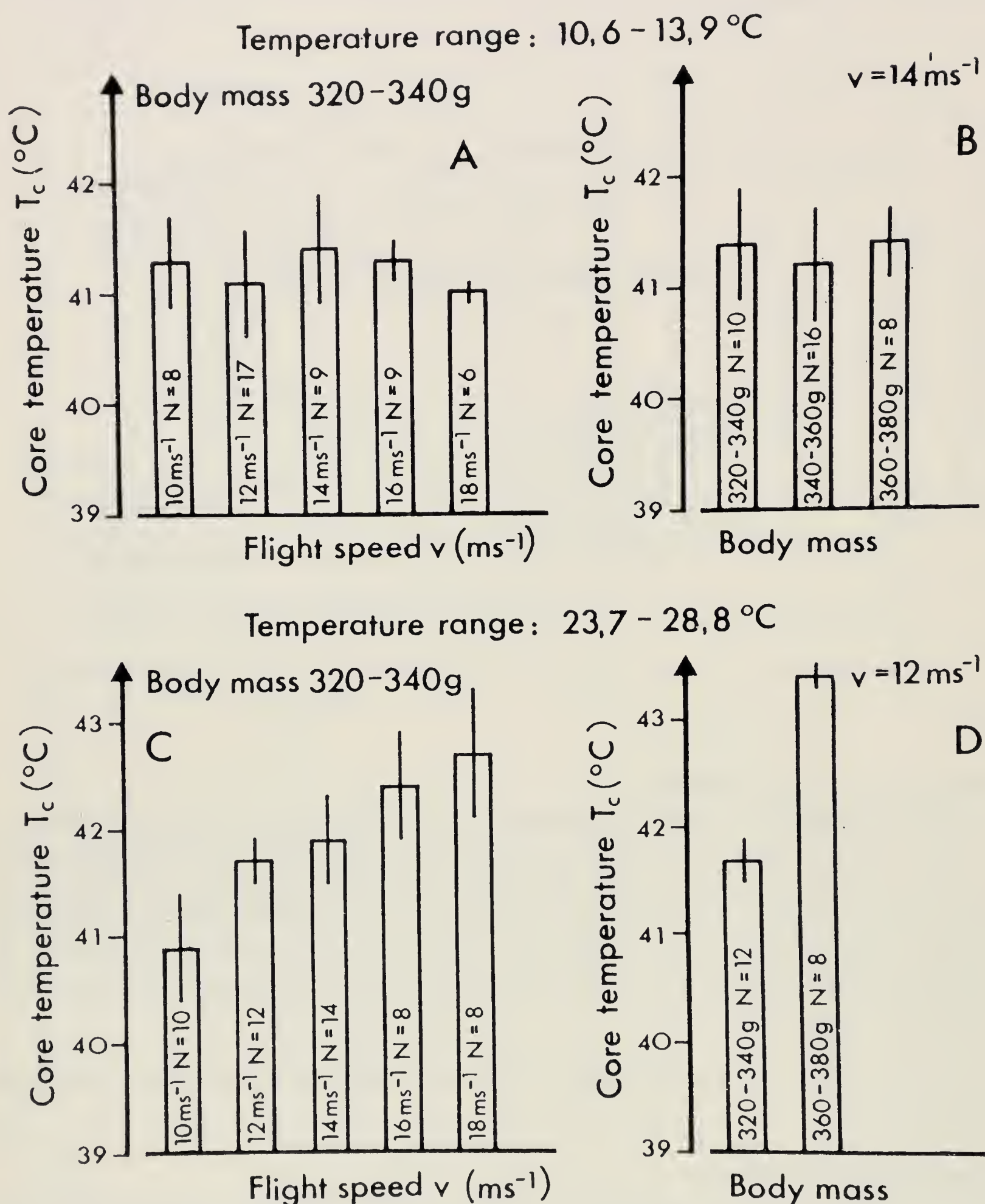


FIGURE 3 - Average core temperature T_c of pigeons during wind tunnel flight. The core temperature is independent of the flight speed (A) and body mass (B) at low ambient temperatures. At high ambient temperatures, the mean core temperature rises with flight speed (C) and body mass (D). Marks: standard deviation.

gliding phases at wind speeds of 10–14 ms⁻¹ and continuous beating at speeds above 14 ms⁻¹. When ambient temperatures were high, birds with extra high body mass and/or at especially high flight speeds showed an increasing tendency towards flying irregularly and attempting to land. On such occasions the birds were seen to pant and spread their wings after landing. Sometimes signs of thermoregulatory behaviour (e.g. beak opening, lowering the legs which are usually tucked under their feathers during

flight (Biesel & Nachtigall 1987)) were observed. The flight times at high ambient temperatures (24 - 29.1°C) were normally shorter (23.1 min \pm 8.7 min; n = 11) than at lower ambient temperatures (10.6 - 16.5°C; 57.6 min \pm 11.2 min; n = 22).

As soon as the upper speed limits at which the bird could still carry out stationary thermoregulation were known, care was taken to remain below these speeds when metabolic rate measurements were being carried out.

Time functions of core measurements

Figures 2b, 2c show the time functions of the core temperature T_c and ambient temperature (wind temperature) T_a from two flights at high and low T_a . T_c remained more or less constant around 40°C during the pre-flight resting period, independent of T_a . After flying had started, T_c increased by a few degrees (1.5 to 3.0°C) and reached a new stationary value after 6 to 10 minutes of flight. An increase or decrease in flight speed resulted in T_c increasing or decreasing accordingly until a new constant value was obtained. After flight, T_c decreased more or less exponentially to the value before flight began.

Core temperature during rest

The average core temperature T_c during rest was 39.8°C \pm 0.7°C (n = 48). A statistically significant ($P=0.05$) correlation between T_c and T_a was not found in the T_a range studied. Thus the core temperature remained independent of the wind temperature and was not influenced by the cooling effect of wind flow.

Core temperature during flight

T_c increased during flight. At an optimal flight speed of 12 m s⁻¹ T_c lay between 39.7 and 43.3°C (minimum and maximum values measured). During flight T_c increased significantly ($P = 0.05$) and linearly with T_a within the temperature range studied. Thus a higher hyperthermia (difference between flight T_c and resting T_c) occurs when the ambient temperature rises, i.e. around 1.4°C at $T_a = 10^\circ\text{C}$ and around 2.3°C at $T_a = 30^\circ\text{C}$.

Within the speed range of $10 \leq v \leq 18$ m s⁻¹ tested, the mean core temperature was independent of flight speed v as long as the ambient temperature was low (10.6 - 13.9°C). At higher ambient temperatures (23.7 - 29.1°C) T_c increased with v significantly ($P = 0.05$) and linearly : T_c (°C) = 0.22 v (ms⁻¹) + 38.8. Furthermore, flight values of T_c were higher in animals which had a heavier body mass due to feeding before a flight experiment, but this effect was only noticeable at higher ambient temperatures (Figure 3 a-d).

DISCUSSION

Core temperatures compared with measurements by other authors

The resting core temperature values of 39.8 \pm 0.7°C of our pigeons were similar to those measured by Bernstein (1974), but clearly lower than values obtained by Hart and Roy (1967), Aulie (1961) and Butler et al. (1977). Compared to these data the values of 43.3 to 44.5°C measured by Butler et al (1988) appear to be extremely high. These measurements were all obtained from very short flights. They lasted on an average less than 10 minutes and in some case even under 2 minutes because the

birds refused to fly longer. Their behaviour after landing (panting and wing spreading) was typical for overheating.

One may say that these pigeons were unsuitable for wind tunnel flight and not sufficiently trained and therefore, the measurements do not represent quasi-natural conditions. On the contrary the core temperature of our pigeons which flew non-stop for more than three hours in a wind tunnel (with an optimal speed of 12 ms^{-1} and normal body mass), remained constant at low ambient temperatures.

In our experiments, unphysiologically high T_c values and symptoms of overheating only occurred when ambient temperatures were high, and the additional stress of high flight speed (Figure 3c) and/or too high body mass (overfed birds or birds with their crops full) was given (Figure 3d). Even then, maximum core temperatures of around 43.5°C were not as high as those obtained by other authors in pigeons (and other birds; not discussed here).

Nevertheless, an increase in resting values compared to flight values was found in all test cases; in our case hyperthermia was 1.5 to 2.5°C at $10^\circ\text{C} \leq T_a \leq 30^\circ\text{C}$. These values are not excessive, do not reflect unphysiological situations and can be held constant for hours without any apparent difficulty.

Meaning of hyperthermia

The importance of a constant hyperthermia may lie in the fact that, obviously due to enzymatic activation, a higher muscle temperature increases the maximum performance output and possibly the muscle efficiency as well, in man (Torre-Bueno 1976). This would have a great advantage for birds if it were valid for them too. A bird would then be able to fly just as efficiently with less muscle mass and thus fly for greater distances during long distance flight with the energy reserves available. The hyperthermia observed would therefore have more of a working physiological function than of a heat regulatory one, and is nevertheless important for extremely long migration flights. The excessive hyperthermia which depasses the physiological, stationary values and only occurs under the above mentioned stress-conditions, can hardly be explained as being other than an emergency mechanism to dispose of excess heat for a short time.

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ON THE AERODYNAMICS OF THE TAIL IN BIRDS

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ABSTRACT. Windtunnel experiments have been carried out on a rectangular wing for a large variety of tail planform shapes and deflection angles as well as for twisted tails in symmetrical and unsymmetrical free stream flow. As in airplanes the tail of a bird acts as a device to maintain longitudinal and lateral stability and control. Adding a tail to a wing leads to an increase of longitudinal stability. Whereas in airplanes lateral stability is performed mainly by means of a vertical fin, in birds the same is achieved by twisting the tail. Concerning control of the longitudinal motion deflections of the tail up and down change lift and pitching moment, and the corresponding effectiveness is governed by size and aspect ratio of the tail. Control of the lateral motion in airplanes is effected by side forces and yawing moments due to the deflection of the rudder of a vertical fin. In birds, however, such forces and moments are again produced by twisting the tail, which leads to a lateral component of the tail force.
Keywords: Aerodynamics, control, stability, tail.

INTRODUCTION

Stability and control of airplanes are maintained by small additional lifting surfaces which are usually positioned downstream of the wing. A horizontal wing stabilizes the longitudinal motion and a flap at this wing acts as an elevator to control the pitching moment. Concerning the lateral motion a vertical fin leads to increased directional stability and a rudder at this fin is used to control the yawing moment, whereas control of the rolling moment is mainly achieved by deflections of the ailerons at the main wing. In birds, however, the situation is different. Birds have at first glance no vertical fin and the small additional horizontal wing is attached to the trailing-edge of the main wing as a tail.

It is common understanding since a long time (Stresemann 1934, Ruppel 1975, Oehme 1976b, Nachtigall 1985, Burton 1990) that deflections of the tail up and down act as an elevator to control the longitudinal motion. The effects of length, size and shape of the tail relative to the wing on the control effectiveness are unknown and systematic investigations on this subject are missing. Concerning lateral control twisting of the tail has been explained as a device to produce a rolling moment (Oehme 1976a,c, Nachtigall 1985) and other effects have not yet been discussed so far. The important contribution of a tail to the longitudinal and lateral stability has not been considered. Therefore the present knowledge on the aerodynamic effects of a tail is at low standard and systematic investigations are urgently needed.

METHODS

Comprehensive experimental investigations have been carried out in the 1.3m low speed windtunnel of Institut für Strömungsmechanik at Technische Universität Braunschweig, Germany. A rectangular wing, having an aspect ratio (span/chord) A

$= b/c = 5.0$ and a NACA 3412 airfoil, has been equipped with a series of 26 tails. Length, size and lateral spreading have been varied systematically including forked planform shapes. Three-component balance measurements have been carried out for all these wing-tail configurations for plane (untwisted) tails and for different tail deflections up and down. For one typical tail planform shape, which will be discussed subsequently, also a twisted tail has been investigated. In this case six-component balance measurements have been performed again for different tail deflections up and down. The Reynolds number was $Re = V c/v = 3.7 \cdot 10^5$.

Following here the results for only one wing-tail configuration (called tail B) both untwisted and twisted are demonstrated to show the basic contributions of a tail to longitudinal and lateral stability and control. The comprehensive results on the effects of tail planform shape on these contributions will be published elsewhere.

RESULTS

The rectangular wing and the tail of shape B are shown in Figure 1. The length l and the width $2a = 2f$ of this tail are equal to the chord length c of the wing ($l/c = 1.0$, $f/a = 1.0$, $a/c = 0.50$) and the tail area S_T is therefore 20 % of the wing area S_w . Without a deflection up or down the tail is represented by a flat plate which is adjusted tangential to the centre line of the airfoil NACA 3412 at the trailing-edge of the wing. The diagram in Figure 1 shows the lift coefficient $c_L = 2L/\rho V^2 S$ (L lift, ρ density of the air, V free stream velocity, S area of wing or area of wing plus tail) and the pitching moment coefficient about the quarter chord point $c_m = 2M/\rho V^2 S \bar{c}$ (M pitching moment nose-up positive, \bar{c} reference chord) as functions of the angle of attack α .

The results for the wing alone are discussed first. Lift and pitching moment depend linearly on the angle of attack and the departure from this behaviour at high angles of attack is due to flow separations. The pitching moment slope dc_m/dc_L turns out to be positive. With increasing lift the nose-up pitching moment increases as well and this leads again to an increase of the angle of attack. This means that the wing alone is unstable.

By adding the tail B to the wing the lift L as well as the area S increase. Since the lift coefficients of the wing-tail configuration are lower than those for the wing alone one can conclude that the generation of lift by adding a tail to the wing is very ineffective. This is due to the fact that the tail works in a downwash field which is induced by the wing. Concerning the pitching moment the slope dc_m/dc_L is now negative for the wing-tail configuration. This means that the wing-tail configuration is stable. By adding the tail to the wing longitudinal stability is considerably improved.

By deflections of the tail up ($\varepsilon = -5^\circ$) and down ($\varepsilon = +5^\circ$) the lift and pitching moment curves $c_L(\alpha)$ and $c_m(\alpha)$ are shifted parallel. This means that the zero-lift angle of attack α_0 as well as the pitching moment at zero lift $c_{m0} = c_m(c_L = 0)$ can be varied by means of such deflections ε . Therefore the tail of a bird acts as an elevator to control the longitudinal motion. For a given position of the centre of gravity an equilibrium state can be achieved by a proper adjustment of the deflection angle ε . The pitching moment slope dc_m/dc_L remains constant for different deflection angles ε . This means that the longitudinal stability is kept for different tail deflections.

$A = b/c = 5.0$
 $a/c = 0.5$
 $f/a = 1.0$
 $l/c = 1.0$

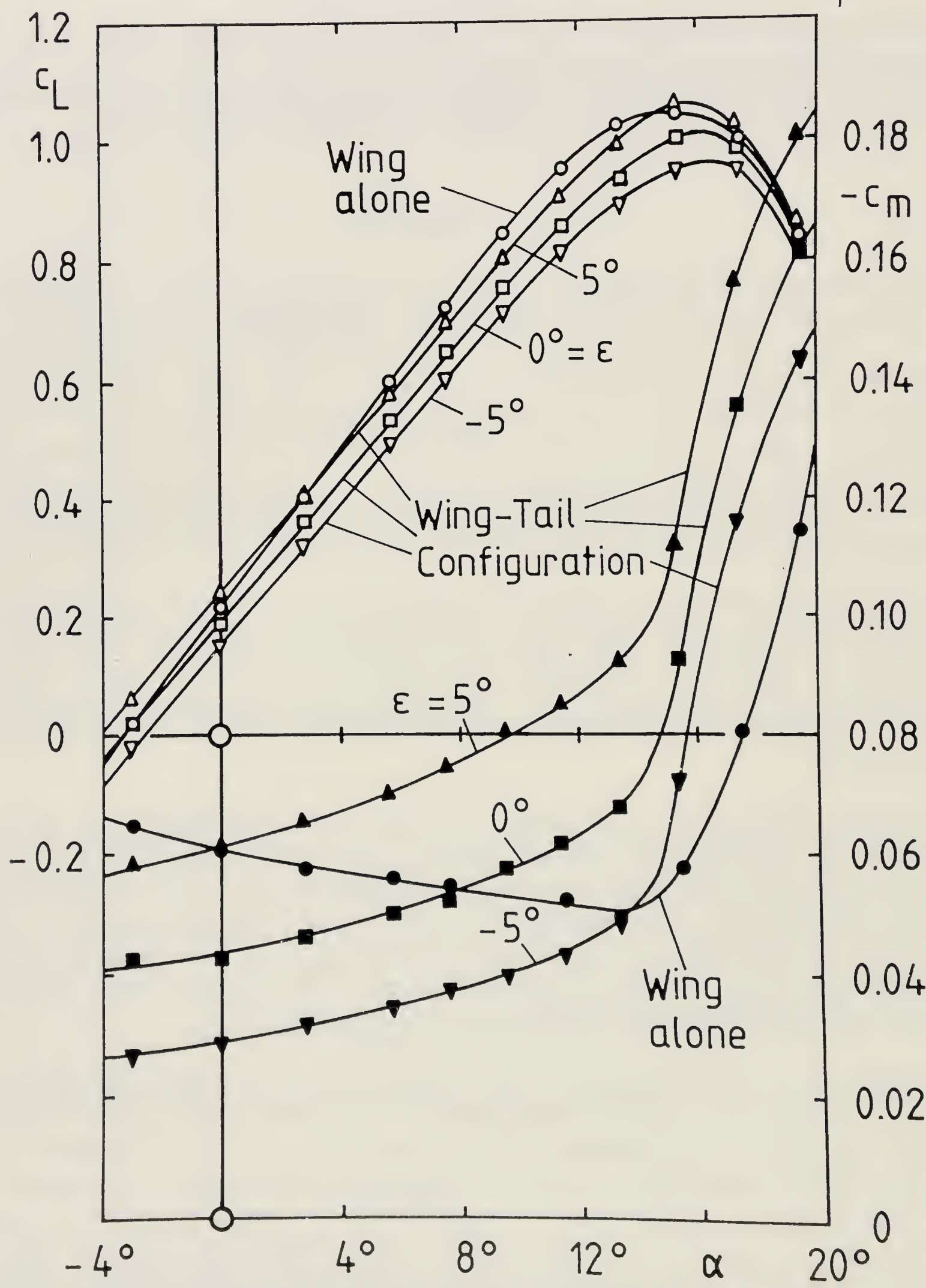
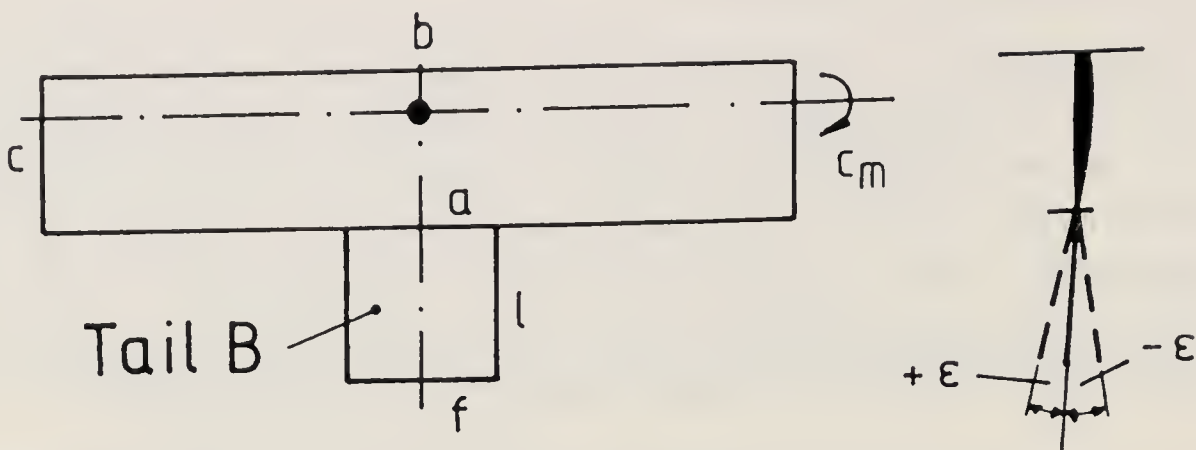


FIGURE 1 - Aerodynamic characteristics of wing and untwisted wing-tail configurations in symmetrical flow (Tail shape B)

The wing alone as well as the wing with an untwisted ($v = 0^\circ$) and with a twisted ($v = 30^\circ$) tail of shape B have also been tested in unsymmetrical free stream flow. The results are shown in Figure 2. In the diagrams rolling moment coefficient $c_l = 4R/\rho V^2 S b$ (R rolling moment, b span), yawing moment coefficient $c_n = 4N/\rho V^2 S b$ (N yawing moment) and sideforce coefficient $c_y = 2Y/\rho V^2 S$ (Y sideforce) are plotted against the angle of sideslip β for a constant angle of attack $\alpha = 9.5^\circ$.

The results for the wing alone are described first. In symmetrical free stream flow ($\beta = 0^\circ$) all coefficients are zero. For a positive angle of sideslip $\beta > 0^\circ$ the lift on the windward half is larger than that on the leeward half of the wing. This leads to a negative rolling moment and the rolling moment derivative is $dc_l/d\beta < 0$. Since the local drag is correlated with the local lift the drag on the windward half is also larger than that on the leeward half of the wing. A positive yawing moment with a derivative $dc_n/d\beta > 0$ results which is called stable because it has the tendency to reduce the angle of sideslip. The wing alone shows small directional stability. Concerning the sideforce the present windtunnel model showed a very small positive sideforce with a derivative $dc_y/d\beta > 0$ which is due to the local shape of the wing tips.

Adding an untwisted ($v = 0^\circ$) tail of shape B to the wing leads to the same lateral aerodynamic characteristics as for the wing alone. Therefore an untwisted tail has virtually no effect at all on stability and control of the lateral motion.

If the tail is twisted ($v = 30^\circ$) even in symmetrical free stream flow $\beta = 0^\circ$ a negative rolling moment turns out which has already been described in the literature (Oehme 1976a, Nachtigall 1985). In addition to this, however, a positive sideforce occurs which acts at the tail and therefore also a corresponding negative yawing moment is found. This means that twisting the tail is a measure to produce rolling moments, yawing moments and sideforces simultaneously. The magnitude of these forces and moments depends linearly on the angle of twist of the tail. If the direction of the twist would be altered (e. g. to $v = -30^\circ$) the sign of all three lateral derivatives c_l , c_n and c_y at zero angle of sideslip $\beta = 0^\circ$ would change as well. If the twisted tail ($v = 30^\circ$) is deflected up ($\varepsilon = -5^\circ$) and down ($\varepsilon = +5^\circ$) in symmetrical free stream flow $\beta = 0^\circ$ the lateral derivatives c_l , c_n and c_y vary considerably. Due to the deflection ε the loading of the tail is changed primarily: for increasing deflection angle ε the forces acting on the tail increase. Since the tail is twisted the positive sideforce as well as the corresponding negative yawing moment increase also. The slight variation of the rolling moment due to changes of the deflection angle ε is caused by the sideforce acting below the moments reference point. The results of the present investigations for symmetrical free stream flow $\beta = 0^\circ$ show that a tail twisted in both directions and deflected up and down acts as a device to control the lateral motion.

Other effects of twisting the tail may also be taken from Figure 2 if the variations of the lateral derivatives with the angle of sideslip are taken into account. Concerning the rolling moment the $c_l(\beta)$ curves for all twisted tails ($\varepsilon = -5^\circ, 0^\circ, +5^\circ$) are shifted parallel as compared with the untwisted tail or the wing alone. The stability derivative $dc_l/d\beta$ is not changed by twist v and deflection ε . For yawing moment and sideforce however the situation is different. For a twisted tail ($v = 30^\circ$) the sideforce decreases linearly with increasing angle of sideslip. The stability derivative is $dc_y/d\beta < 0$ and its value is independent of the deflection angle ε . This means that the slightly unstable situation for the wing alone and the untwisted tail has changed towards a stable

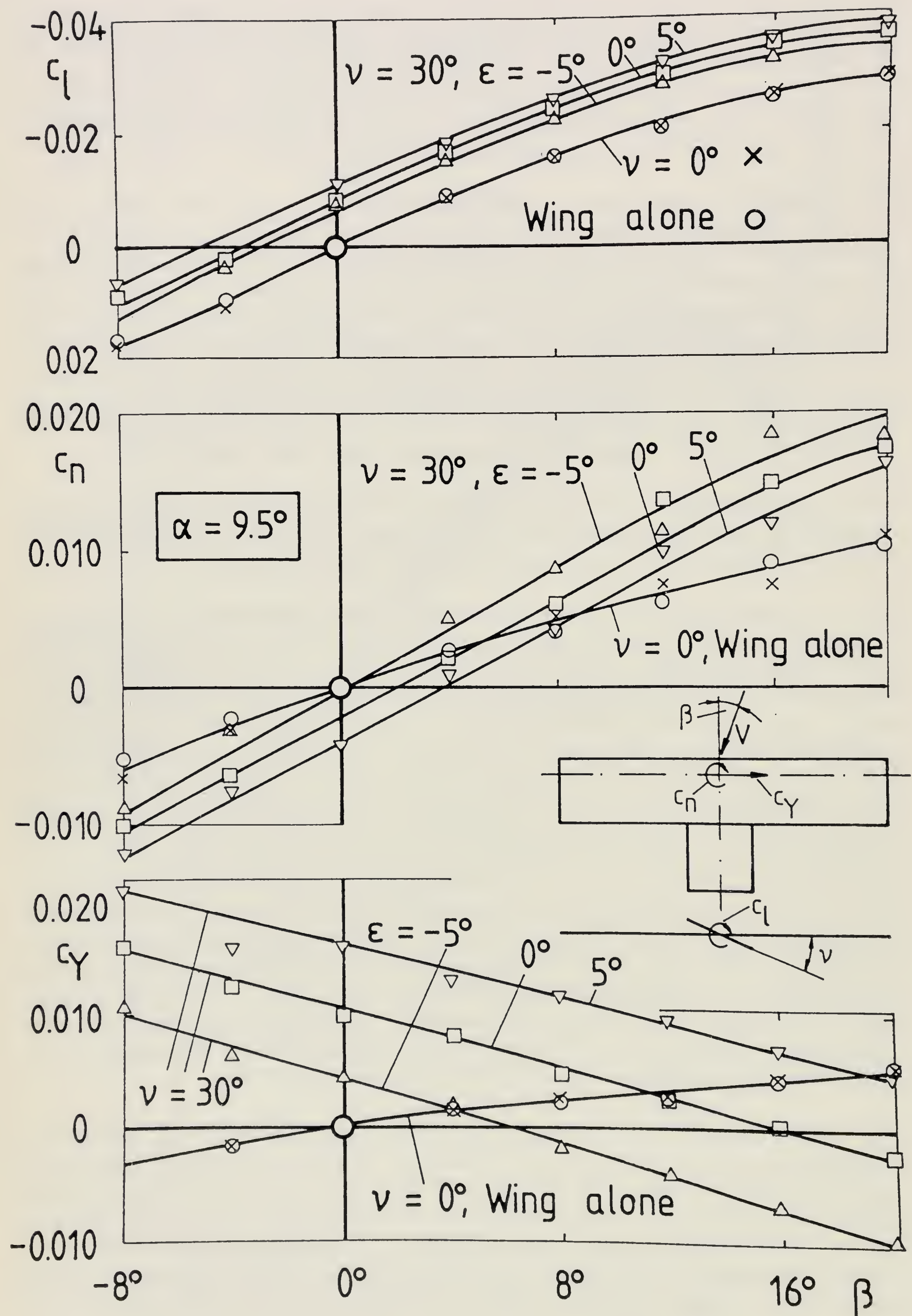


FIGURE 2 - Aerodynamic characteristics of wing, untwisted and twisted wing-tail configurations in unsymmetrical flow (Tail shape B)

behaviour of the configuration with a twisted tail. Similar effects can be seen from the yawing moment results $c_n(\beta)$. The reduction of the sideforce leads to additional positive yawing moments with increasing angles of sideslip. This means that the stability derivative $dc_n/d\beta$ is increased in comparison with the wing alone and the untwisted tail. In the present case the directional stability is considerably improved by the twisted tail and the amount of stability is the same for all deflection angles ε . If the direction of the twist is changed (e. g. to $v = -30^\circ$) there is no effect on the directional stability. This is due to the fact that only the variation of the aerodynamic coefficients with the angle of sideslip has to be taken into account. At an angle of sideslip $\beta > 0$ a crossflow in $-y$ direction takes place which causes an additional positive lift on the tail for $v < 0$ and additional negative lift on the tail for $v > 0$. The reduction of the sideforce with increasing angle of sideslip is caused by the "cross flow drag force" which acts at the tail in $-y$ direction in both cases $v > 0$ and $v < 0$. This means that twisting the tail leads to increased lateral stability and this improvement is independent of the direction of twist.

DISCUSSION

The present investigations have shown that longitudinal stability is achieved and lateral stability is considerably improved by adding a twisted tail to a wing. These benefits occur simply by the presence of the tail with a certain planform shape and an angle of twist for any deflection angle and for any direction of twist. The improvements in longitudinal stability depend on size and planform shape of the tail, whereas those in lateral stability are additionally governed by the amount of twist lv .

The longitudinal and the lateral stability discussed so far are called "static" stabilities. They relate the final flow status of the configuration to the original one in the case of a disturbance. Between these two states a time-dependent dynamic process takes place which is governed by the aerodynamic derivatives as well as by the inertia moments of the configuration. Aperiodic as well as oscillatory motions do occur and they can be both stable or unstable. This kind of dynamic stability is also very important, but it has not yet been investigated in birds.

Deflections of the tail up and down as well as twisting the tail in both directions can be used to control the longitudinal and the lateral motion simultaneously. The main effects of deflections ε up and down are changes of the pitching moment to control the longitudinal motion. Sideforces and yawing moments can be achieved by twisting the tail. It is important, however, that the tail carries some loading in order to be effective. For a positive tail loading positive twisting leads to a positive sideforce and to a negative yawing moment. An unloaded twisted tail produces no sideforce and no yawing moment. For a negative tail loading which is achieved for very large negative deflection angles ε negative twisting leads again to a positive sideforce and to a negative yawing moment. Both ways to produce a positive sideforce at the tail lead to different pitching moment characteristics which influence again the longitudinal control. In birds movements of the wings forwards and rearwards can also be used to achieve longitudinal control.

Compared with airplanes stability and control of the longitudinal motion in birds is achieved in the same way by means of a horizontal tail behind the wing which can be deflected up and down. For the lateral motion however the means are different. In airplanes a vertical fin with a rudder is used to achieve lateral stability and control. In

birds the role of the fin with rudder is adopted by a tail which is twisted in the proper direction according to the tail loading.

Stability and control are strongly dependent on the size and the shape of the tails. The present investigations contain already a large amount of material and results related to the longitudinal motion which will be published elsewhere. Concerning the lateral motion the windtunnel experiments will be continued to include twisted tails with different planform shapes.

CONCLUSIONS

Windtunnel experiments have been carried out on a rectangular wing with tails in symmetrical and unsymmetrical free stream flow. Plane and twisted tails with deflections up and down have been investigated. The following results have been found:

- 1) The presence of a tail in birds increases the stability of the longitudinal motion as in airplanes.
- 2) The tail in birds acts as an elevator as in airplanes. Its effectiveness is governed by size and planform shape, but details are not discussed in this paper.
- 3) Twisting a tail in any direction increases the directional stability of the lateral motion. This measure is used by birds instead of the vertical fin of airplanes.
- 4) Twisting a loaded tail leads to a sideforce and to a yawing moment. Their directions depend on the combination of loading and twist. This measure is used by birds instead of the rudder on the vertical fin of airplanes.

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TIME PATTERN OF WING MOTION DURING CRUISING FLIGHT AND ITS IMPORTANCE FOR FLIGHT ENERGETICS

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ABSTRACT. Alternation between powered and non-powered flight is frequent among birds. Two main forms occur characterized by the course of the non-powered part: the true gliding and the ballistic bounding flight. Two topics are discussed on the basis of model calculations: the overall energy saving and its role with respect to strain of the muscular apparatus. Intermittent flight reduces the cost of transport in comparison with sustained flapping flight of equal horizontal velocity. This saving is purchased by increasing power expenditure during the flapping periods. Within species-specific speed ranges birds may fly with the same cost of transport by variation of time pattern of intermittent flight.

Keywords: Flight energetics, energy saving, intermittent flight.

INTRODUCTION

The optimal utilization of flight ability is determined by two tendencies: minimizing of the energetic cost of transport and prevention of overstressing of the flight muscles. These tendencies are partially directed against one another and the exercised modes of flying are certainly a compromise between them. Several birds cover large distances by sustained flapping flight, e.g. loons, grebes, ducks, geese, waders, and auks. On the other hand we find the dominance of non-powered flight as genuine soaring in larger birds, e.g. albatrosses, petrels, storks, eagles, and vultures. However, a considerable number of species show a more or less regular alternation of powered and non-powered legs during cruising. We find this phenomenon in larger and smaller birds of different taxonomic position. Questions of the energy regime of this alternating or intermittent flight are the subject of this paper. The investigations are more abstract for the present but they try to take into consideration morphological and kinematical characteristics of real species.

PRINCIPLES OF MODEL CALCULATIONS

Flight styles

Four flight styles are distinguished and compared (see Figure 1). Style 1 (not figured) is the non-accelerated, horizontal, sustained flapping flight which presents itself as the theoretical reference of the styles of intermittent flight. Style 2 is a flight without alteration of height but with changing air-speed. Compared with Style 1 the peculiarity is, at the same average velocity, the increase of thrust during the powered flight period which is simultaneously the period of acceleration. Powered part (T_{pow}) and gliding part (T_{gl}) compose the macrocycle (T_{mcyc}). The gliding period is the part of deceleration and requires continuous increase of the lift coefficient in the wings with decreasing air-speed. Style 3 (undulating flight) is a flight with alteration of height but with constant air-speed during both periods of the macrocycle. Since the powered part is climbing flight thrust is also increased compared with that of Style 1. Style 4 (bounding

flight) is similar to Style 3 but besides the change of height there is also a change of air-speed during the glide period which represents a ballistic curve where the wings are folded and drawn close to the body. A small lift force is generated by the trunk in the acceleration phase of the glide period.

Forces, power, cost of transport

Calculation of power requirements was carried out as described elsewhere (Oehme 1985a,b, 1986). The mechanical power of the "engine" sensu *Musculus pectoralis* is computed from kinematical and morphological data (air-speed, angular velocity of the wings, duration of downstroke and beating cycle, wing length, halfspanwise distribution of chord length, mass). Mechanical work done during the upstroke is neglected. A further simplification is that a constant lift coefficient (C_L) is used over the wing length. Hence the spanwise distribution of circulation is only determined by the kinematical and geometrical data just mentioned. As to Style 2, for the powered period constant acceleration is assumed in order to calculate the necessary thrust force during the beating cycles. The glide period with its decreasing air-speed and increasing lift coefficient is calculated spotwise for time intervals of 0.002 seconds. The calculation of the ballistic curve of Style 4 with its changing velocities is performed after Vahlen (1942) and Csicsáky (1977) for the same time interval. The mechanical power during the beating cycle (P_{cyc}) times $T (= T_{pow}/T_{mcyc})$ yields the average power of the macrocycle. That divided by the average horizontal velocity (\bar{v}_{hor}) makes the

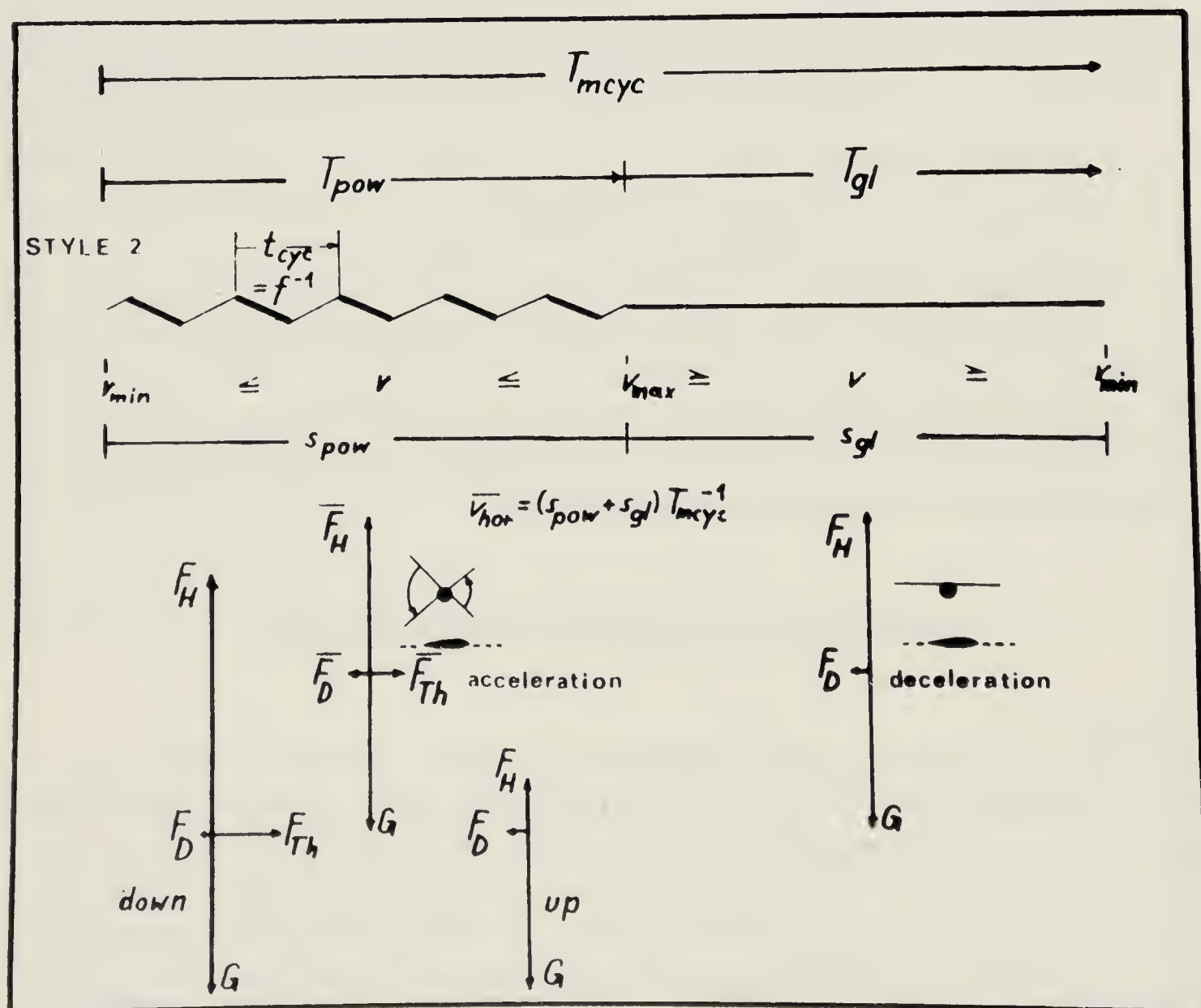


FIGURE 1 - Flight styles. T, t time; v air-speed; s horizontal distance; \bar{F}_H, \bar{F}_H instantaneous and mean aerodynamic force perpendicular to flight path; F_D, \bar{F}_D instantaneous and mean drag; F_{Th}, \bar{F}_{Th} instantaneous and mean thrust; G weight force; f wing beat frequency; h height; Indices: $_{pow}$ powered period, $_{gl}$ gliding period, $_{cyc}$ beating cycle, $_{mcyc}$ macrocycle.

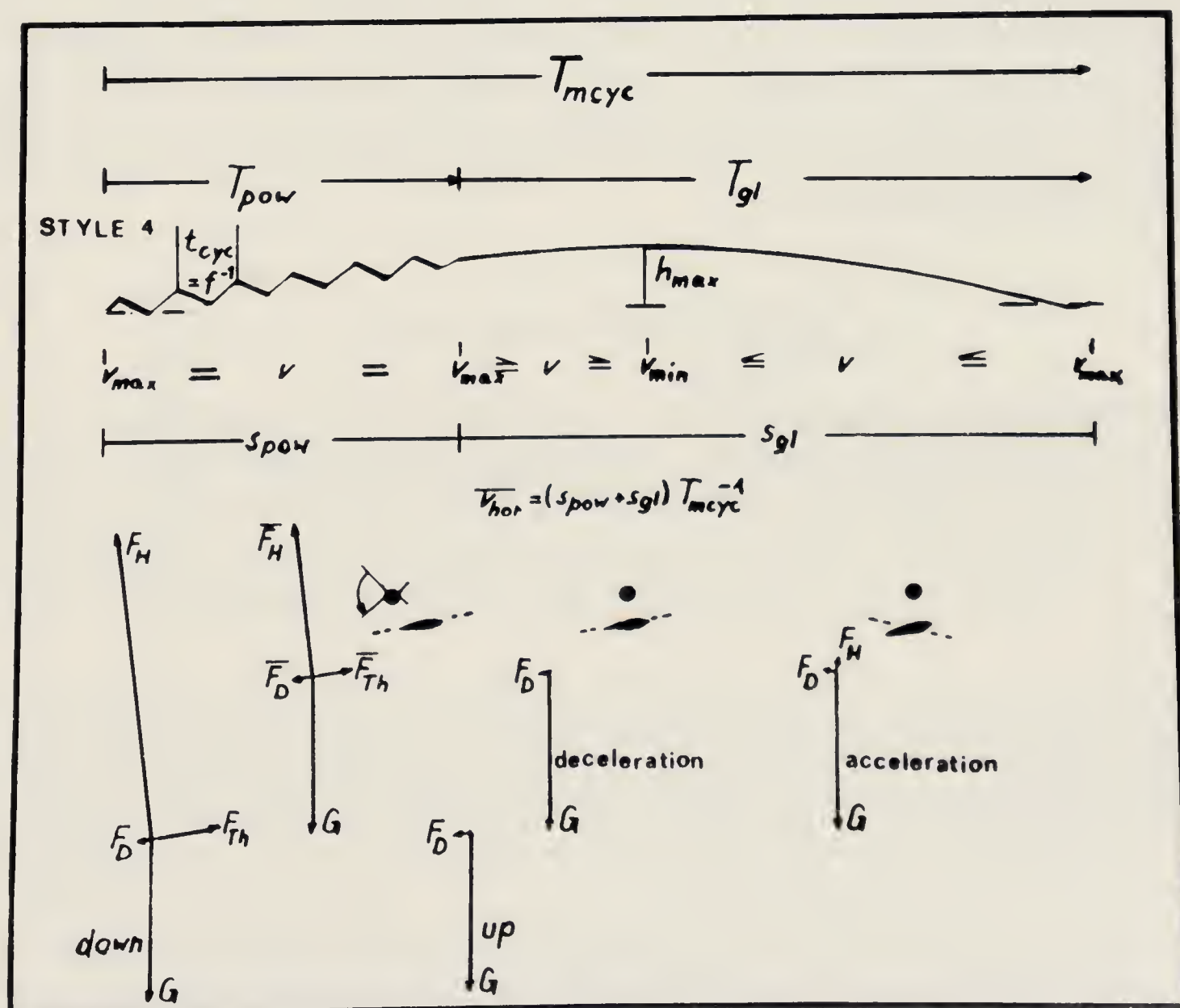
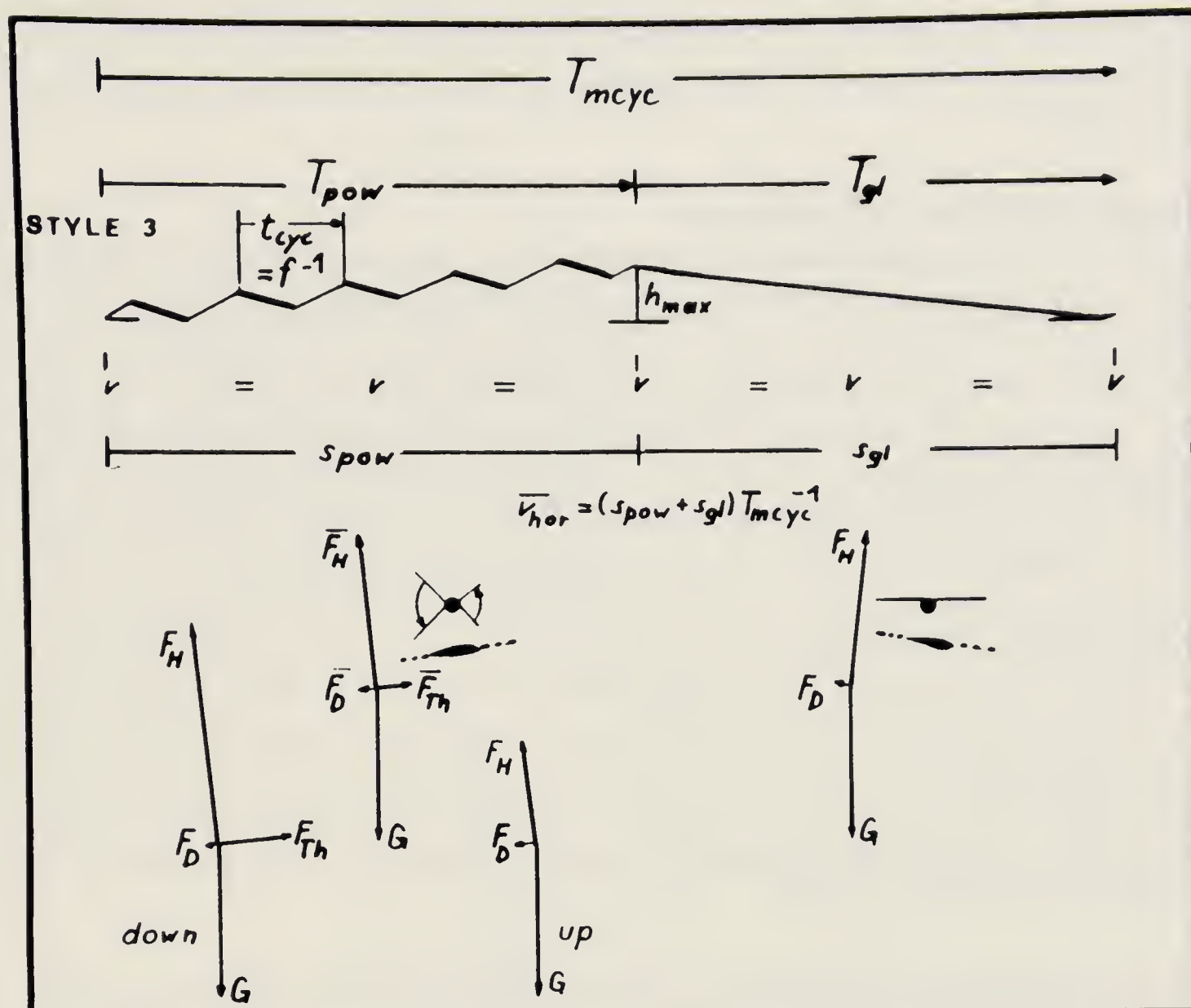


FIGURE 1 – Continued

mechanical cost of transport. To facilitate comparability these quantities are related to body mass: specific power of the cycle (P_{cyc}/m) and specific cost of transport (CT/m), respectively.

Bird models, limits, simplifications

Four models are used, the masses of which differ to the highest by the factor 80 (see Figure 2). Considerable differences exist with the wing load ($mg/(2A_w)$). The wing areas correspond to the outlines given in Figure 2. These are not the natural outlines but they indicate the semispanwise chord length distribution for which the scheme of Oehme & Kitzler (1975) is used. The shaded area of the Models I and II is that which is assumed for lift production during the upstroke. The natural prototypes are: the female Goshawk *Accipiter gentilis* (Model I); the female Common Kestrel *Falco tinnunculus* (Model II); the male House Sparrow *Passer domesticus* (Model III); the female Redstart *Phoenicurus phoenicurus* (Model IV). Masses and principal linear measures are average values based on own measurements and data given in the literature (Glutz von Blotzheim 1971, 1988, Heinzel et al. 1977, Mebs 1989, Peterson et al. 1976, Pforr & Limbrunner 1980). The frontal area (A_b) is assumed as a circle with the largest body width as the diameter. The coefficients for body drag = parasite drag (C_{D_b}) and profile drag (C_{D_p}) were obtained in the Models I and II from gliding with a fineness ratio $\varepsilon = F_D/F_L = 0.1$ supposing minimum induced drag (compare Tucker & Parrott 1970, Videler et al. 1988).

Three limiting values are introduced to test the admissibility of the calculation of the required aerodynamic forces \bar{F}_H and \bar{F}_{Th} in the respective styles and velocities. The lift coefficient must not exceed 1.0 which is a more restrictive precaution (compare Biesel et al. 1985, Knappe & Wagner 1985, Nachtigall et al. 1985). The stroke angle must not exceed 120° . Assuming a uniform relative mass of 17% of both Musculi pectorales in the models the mechanical power output per beating cycle is confined to 30 W/kg in I and II with low stroke frequencies and to 42.5 W/kg in III and IV (compare Weis-Fogh & Alexander 1977).

RESULTS AND DISCUSSION

Examples are shown in Figures 3 and 4; further information can be found in the appendix. The calculations are complex. The duration of the glide period (T_{gl}) along with the given velocity determines the duration of the powered period (T_{pow}) for which, however, only a positive integer of beating cycles is possible. Additionally, in the Styles 3 and 4 there has to be conformity with the climbing angle of the flight path during T_{pow} .

We find that any break of powered flight reduces the cost of transport (CT) and enlarges the instantaneous power of the cycle (P_{cyc}). Energy saving reaches higher amounts in small birds (Style 4) with low velocities than in larger birds which cannot bound. The strength of the reciprocal action between CT and P_{cyc} is characterized by the quota of time of the powered phase $T = T_{\text{pow}}/T_{\text{mcyc}}$. There are only small differences between Style 2 and Style 3 so that a combination of both seems possible. Finally there is some evidence that for a lighter bird with lower stroke frequency it is more difficult to go as fast as a heavier one of about the same size and higher frequency.

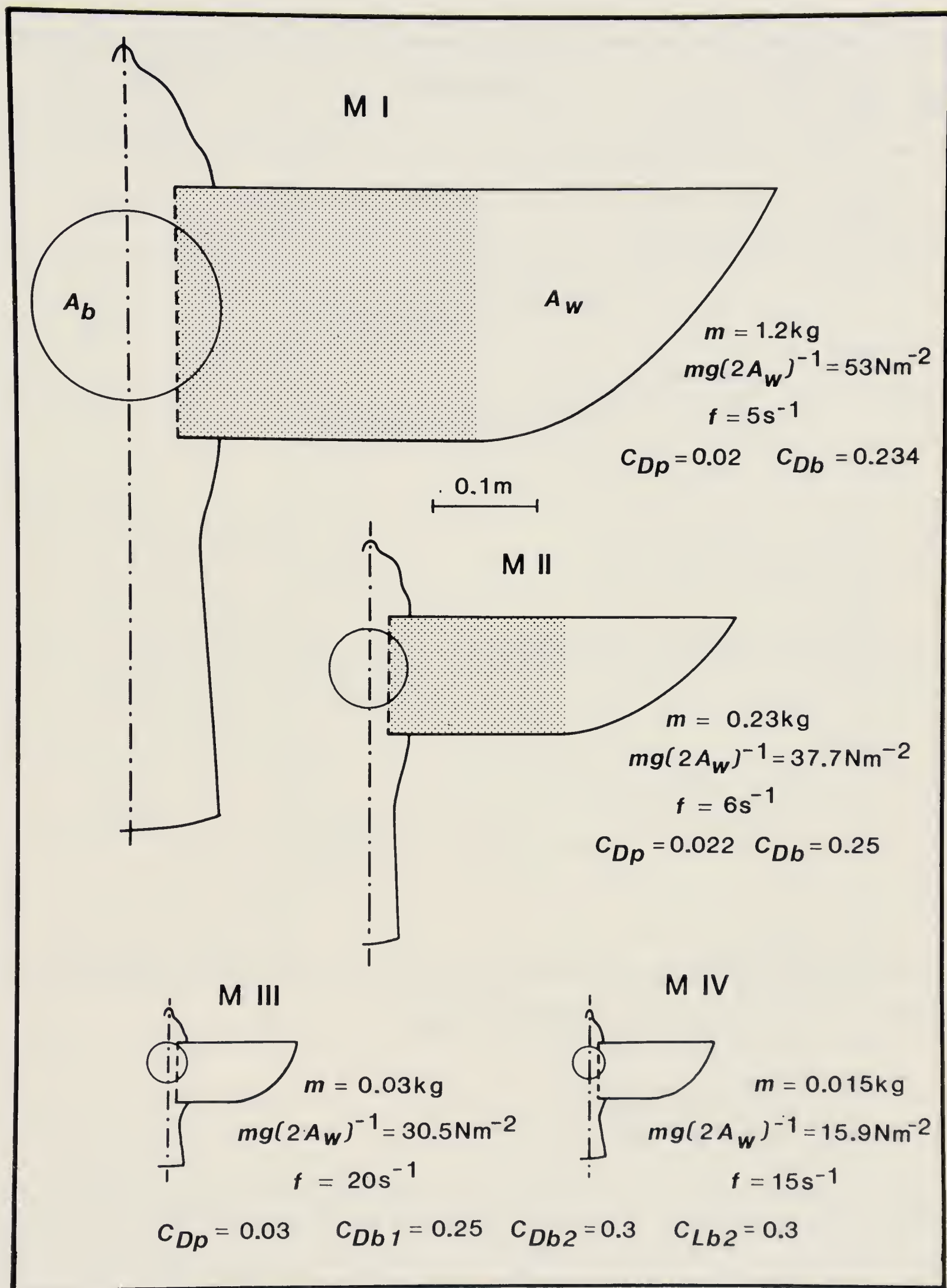


FIGURE 2 – Bird models. C_{Db} coefficient of parasite drag; C_{Dp} coefficient of profile drag; C_{Lb} lift coefficient of body (Style 4); g gravitational acceleration; m mass; A_b frontal area of the body; A_w area of one wing; numerical indices in Models III and IV: gliding periods 1 and 2; see also Figure 1.

One may hypothesize that fattening in migrants is not only the preparation of the necessary fuel but also an improvement of flight performance and thereby of the economy of energy consumption provided that the efficiency of the muscles is adapted to the greater weight.

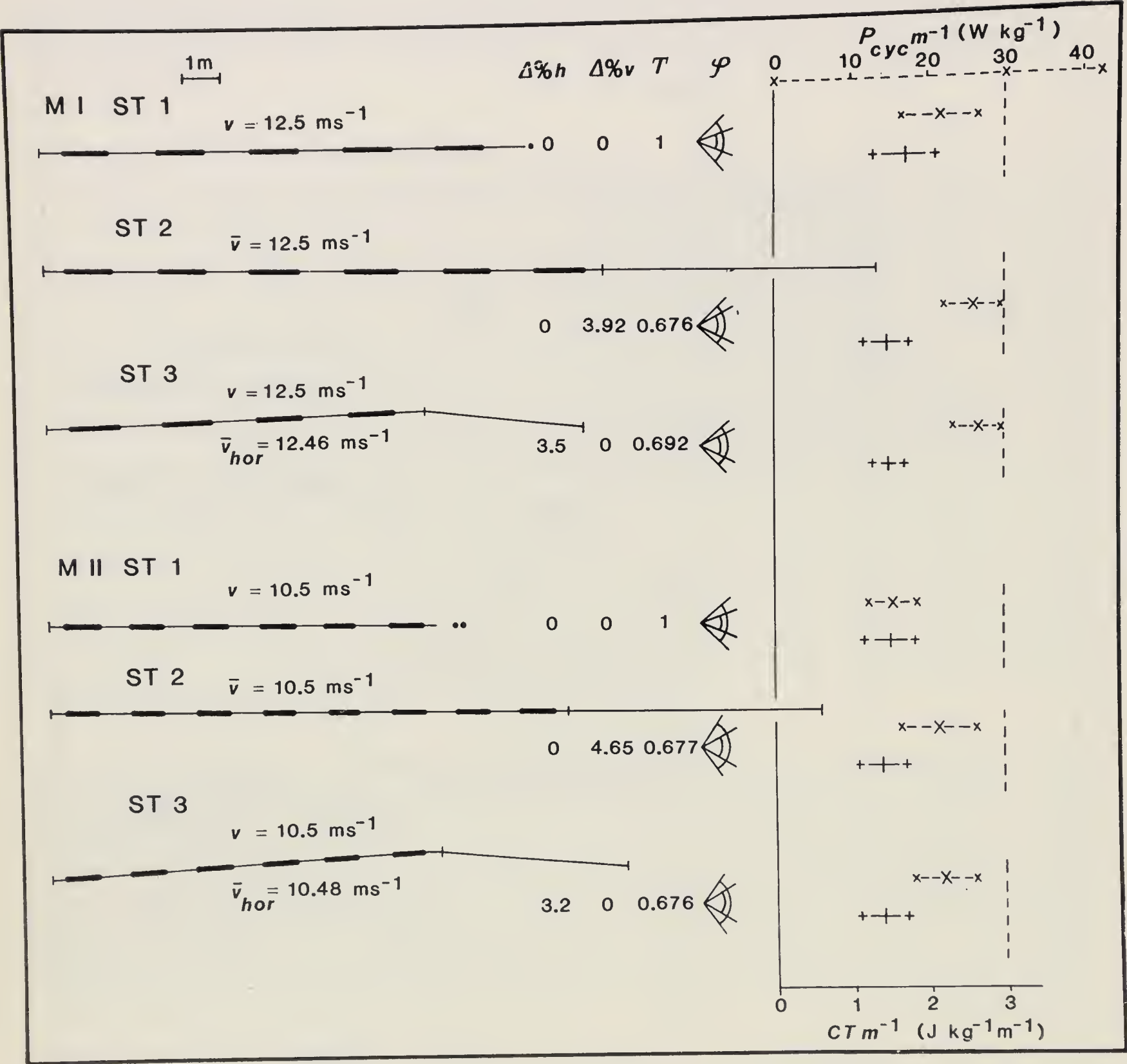


FIGURE 3 - Flight characteristics of Models I and II.

$\Delta\%h = 100 \times h_{max} / (s_{pow} + s_{gl})$,
 $\Delta\%v = 100 \times (v_{max} - v_{min}) / v_{max}$,
 $T = T_{pow} / T_{mcyc}$, ϕ stroke angle;
see also Figure1 and text.

A peculiarity of the results in the Models I and II shall be emphasized. The values of the instantaneous power output (P_{cyc}/m) as well as those of the cost of transport (CT/m) vary within a considerable range. This is why the magnitude of the resulting aerodynamic force perpendicular to the flight path during the upstroke is not fixed (see Appendix, factor k). The stronger this force the more balanced is the average lifting force of the beating cycle which compensates in the main the weight force. This is achieved when the strength of the bound vortex (circulation) is nearly equal in the wings during downstroke and upstroke. But this means an increase of the force directed backwards during the upstroke, say enlargement of the average drag, which must be overcome by stronger thrust of the downstroke. The consequence is an increasing stroke angle and higher power output compared with a beating mode where the lifting force during the upstroke is smaller. In larger birds with low wing beat frequency the vertical upward force during the upstroke must be logically as high as

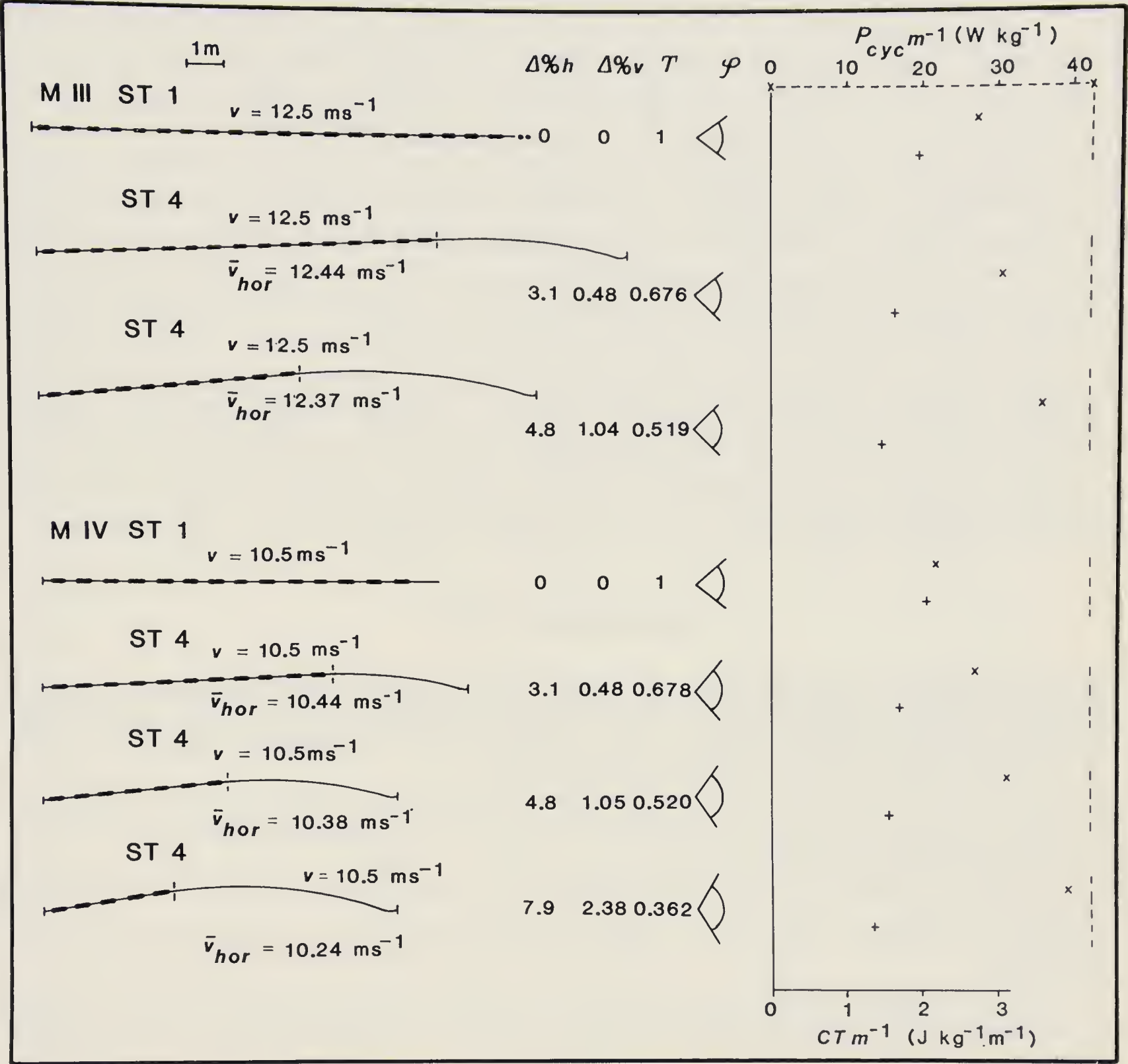


FIGURE 4 - Flight characteristics of Models III and IV. See Figure 3.

possible at low velocities. The smaller the bird and the higher, then, as a rule, the frequency the more the generation of the lifting force of the cycle can be concentrated in the downstroke (e.g. Models III and IV with Style 4). Therefore an appropriate staggering of the circulation between the stroke phases may be advantageous. This may be attached to the average values of the Models I and II. Thus neither the “motor” will be stressed up to its limit of mechanical performance nor will the lift coefficient reach its upper limit. In the Models III and IV, bounding flight (Style 4), one should reckon with deviations from the ascending flight path of the powered phase as a straight line. It may take the form of a stretched lying sigmoid curve without a decisive change of the facts of the case. But never does the powered phase of the macrocycle start in a downwards directed part of the flight path as it is represented by Rayner (1977) and Norberg (1990). This statement is based on cinematographical investigations on the flight of titmice, redstarts, sparrows, and finches.

The time ratio T indicates the degree of energy saving. The magnitude of CT-reduction when compared with the sustained horizontal flapping flight is negatively correlated with T . It can only decrease at a given air-speed as far as the aerodynamical

(C_L) and the myomechanical (P_{cyc}) limits are not passed over. But T is not only responsible for optimizing the gross energy economy but also for the subtle function of the "flying motor". Low T means longer breaks for restitution of adenosine triphosphate in the myofibrils. On the other hand a minimum T implies the entire exhaustion of the physiological performance during the flapping phase of the macrocycle. Between these constraints a compromise will be established which will tend to smaller or larger T in dependence on the specific constitution of the muscle. Furthermore we see that the bird has ranges of velocities and time patterns within which it can realize its flight tactics. The postulate possibly fails that energy saving should be only feasible if the velocity of the alternating flight is higher than the theoretical optimum velocity for minimum cost of transport in sustained flapping flight (Rayner 1977, Norberg 1990). On the contrary the bird may fly with equal cost of transport by variation of speed and adequate variation of the time pattern. Then, for the real flying behaviour a fixed "maximum range speed" s.str. does not occur. This could correspond to a statement of Wieser (1986) with this tendency whereas the plain relation between mass and mechanical flight power output by the same author yields much too low values.

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APPENDIX

Flight characteristics of the four bird models at different velocities. STY flight style; N number of cycles of the powered period; γ climbing angle; $k = F_H(\text{upstroke})/F_H(\text{downstroke})$; $\Delta\%P_{\text{cyc}}$, $\Delta\%CT$: $100 \times (\text{value of the respective style value of Style 1}) / (\text{value of Style 1})$, in the Models I and II “a” or “b” or “mean” at a time. Explanation of other symbols and abbreviations: see Figures 3 and 4, and text.

STY	v_{max}	$\Delta\% v$	\bar{v}_{hor}	N	γ	$\Delta\% h$	T	k	φ	P_{cyc}/m	$\Delta\%P_{\text{cyc}}$	CT/m	$\Delta\%CT$
1	10.5	0	10.5	∞	0	0	1	0.55 0.51	72.7 67.4	21.606 20.302 20.954	- - -	2.058 1.934 1.996	a) b) mean MOD.I
2	10.75	4.65	10.5	8	0	0	0.670	0.52 0.49	85.9 80.6	26.640 25.222 25.931	+23.3 +24.2 +23.8	1.700 1.609 1.654	a) b) mean MOD.I
2	11	9.09	10.5	16	0	0	0.673	0.52 0.49	85.7 80.4	26.548 25.132 25.840	+22.9 +23.8 +23.3	1.702 1.611 1.656	a) b) mean MOD.I
1	12.5	0	12.5	∞	0	0	1	0.56 0.06	87.0 40.0	26.391 16.560 21.476	- - -	2.111 1.325 1.718	a) b) mean MOD.I
2	12.75	3.92	12.5	6	0	0	0.676	0.4-0 0.09	84.7 54.5	28.568 22.335 25.452	+ 8.2 +34.9 +18.5	1.632 1.208 1.420	a) b) mean MOD.I
2	13	7.69	12.5	11	0	0	0.659	0.40 0.09	86.4 55.5	29.130 22.788 25.959	+10.4 +37.6 +20.9	1.536 1.201 1.368	a) b) mean MOD.I
3	12.5	0	12.46	4	2.87	3.47	0.692	0.39 0.06	88.0 55.0	29.932 23.214 26.573	+13.4 +40.2 +23.7	1.662 1.289 1.476	a) b) mean MOD.I

STY	v_{max}	$\Delta\% v$	\bar{v}_{hor}	N	γ	$\Delta\% h$	T	k	φ	P_{cvc}/m	$\Delta\%P_{cvc}$	CT/m	$\Delta\%CT$
1	10.5	0	10.5	∞	0	0	1	0.53	88.0	18.677	-	-	a) MOD.II
								0.12	44.5	12.139	-	-	b) mean
										15.408	-	-	
2	10.75	4.65	10.5	8	0	0	0.677	0.55	114.1	25.966	+39.0	-5.9	a)
								0.09	57.1	16.322	+34.5	-9.0	b) MOD.II
										21.144	+37.3	-7.1	mean
2	11	9.09	10.5	15	0	0	0.666	0.55	114.9	26.258	+40.6	-6.4	a)
								0.09	57.8	16.544	+36.3	-9.3	b) MOD.II
										21.401	+38.9	-7.5	mean
3	10.5	0	10.48	6	2.73	3.23	0.676	0.51	111.2	25.872	+38.5	-6.1	a)
								0.12	63.1	17.695	+45.8	-1.2	b) MOD.II
										21.784	+41.4	-4.2	mean
3	10.5	0	10.45	3	5.47	4.89	0.511	0.40	117.4	29.922	+60.2	-17.8	a)
								0.12	80.5	23.312	+92.0	-1.4	b) MOD.II
										26.617	+72.7	-11.3	mean
1	12.5	0	12.5	∞	0	0	1	0.58	117.9	26.777	-	-	-a)
								0	52.5	16.231	-	-	b) MOD.II
										21.504	-	-	mean
2	12.75	3.92	12.5	5	0	0	0.667	0.32	108.4	28.676	+7.1	-28.6	a)
								0	73.0	23.383	+44.1	-3.9	b) MOD.II
										26.030	+21.0	-19.3	mean
2	13	7.69	12.5	11	0	0	0.672	0.37	115.5	30.028	+12.1	-24.6	a)
								0	72.6	23.229	+43.1	-3.8	b) MOD.II
										26.628	+23.8	-16.8	mean

STY	V_{max}	$\Delta\% v$	\bar{V}_{hor}	N	γ	$\Delta\% h$	T	k	φ	P_{cyc}/m	$\Delta\% P_{cyc}$	CT/m	$\Delta\% CT$
3	12.5	0	12.47	6	2.29	3.90	0.757	0.43	117.8	29.515	+10.2	-16.3	a)
								0	67.6	21.405	+31.9	+ 0.2	b)
										25.460	+18.4	-10.1	mean
3	12.5	0	12.44	3	4.59	4.90	0.610	0.21	105.4	29.976	+11.9	-31.5	a)
								0	81.9	26.635	+64.1	+0.6	b)
										28.306	+31.6	-19.4	mean
1	10.5	0	10.5	∞	0	0	1	0	57.3	17.509	-	-	MOD.III
4	10.5	0.29	10.47	9	2.06	2.45	0.650	0	64.5	21.706	+24.0	-19.2	MOD.III
4	10.5	0.67	10.43	6	3.85	3.73	0.493	0	70.4	25.348	+44.8	-28.3	MOD.III
4	10.5	2.10	10.28	4	8.83	6.34	0.287	0	91.2	35.206	+101.1	-41.3	MOD.III
1	12.5	0	12.5	∞	0	0	1	0	67.8	25.281	-	-	MOD.III
4	12.5	0.48	12.43	17	2.54	3.11	0.676	0	81.7	31.187	+23.4	-16.1	MOD.III
4	12.5	1.04	12.35	11	4.80	4.81	0.518	0	93.2	36.488	+44.3	-24.2	MOD.III
1	10.5	0	10.5	∞	0	0	1	0	80.0	22.109	-	-	MOD.IV
4	10.5	0.48	10.44	11	2.55	3.13	0.678	0	95.0	27.122	+22.7	-16.4	MOD.IV
4	10.5	1.05	10.38	7	4.80	4.82	0.520	0	107.4	31.588	+42.9	-24.9	MOD.IV
4	10.5	2.38	10.24	5	8.75	7.03	0.362	0	120.0	39.273	+77.6	-34.0	MOD.IV
1	12.5	0	12.5	∞	0	0	1	0	115.7	35.079	-	-	MOD.IV
4	12.5	0.96	12.37	19	3.52	4.29	0.670	0	120.0	42.937	+22.4	-17.1	MOD.IV

CONCLUDING REMARKS: BIRD FLIGHT

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It is clear that through sophisticated modelling and the application of new technologies, a balance of theoretical and empirical approaches are contained within the papers of this symposium. The application of flow visualization techniques allows for a description of the wake vortices created by flying birds which in turn, provides for the recognition of gait patterns (Rayner). Why do certain sized birds adopt one gait or another and how does gait selection relate to the evolution of flapping flight? If more than one gait is used by a species, does this require a “shifting-of-gears” from a neuromuscular control standpoint (Goslow)? Nachtigall’s studies stimulate us to wonder once again if the high altitude migrations of geese relate to the temperature control and dissipation of metabolic heat. For years we have wondered why airplanes possess a vertical tail rudder but most birds do not. Hummel’s wind tunnel studies provide us with many answers and more fascinating questions. An issue of long standing interest relates to wing beat frequency and the cost of transport in birds of different locomotor habits (Oehme). Given a theoretical framework from which to work, can we design the appropriate experiments to test the theory?

All of these questions are of great interest and significance for the understanding of bird flight. Much work remains to be done. We would like to thank all participants for their contributions. Special thanks to Dr R. Bannash for his presentation of Prof. Dr Oehme’s paper at the Congress.

SYMPOSIUM 10

NEW ASPECTS OF AVIAN MIGRATION SYSTEMS

Conveners S. B. TERRILL and P. Z. ANTAS

SYMPOSIUM 10

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INTRODUCTORY REMARKS: NEW ASPECTS OF AVIAN MIGRATION SYSTEMS

SCOTT B. TERRILL

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The scientific study of bird migration has diverged into several major lines of research: navigation and orientation, genetics and endogenous rhythms, behavioral ecology, and ecophysiology. All represent areas of current interest and rapid advancement. I think that this symposium will demonstrate not only recent advances in several of these areas, but also how effectively these subdisciplines can be integrated in the advancement of general knowledge of avian migration systems.

The papers in this symposium bring into focus ecophysiology, behavioral ecology and population biology of bird migration. Recognition of the importance of these subdisciplines within the broader scope of bird migration is not necessarily new; in fact, over the past fifteen years the case for the importance of ecological and physiological research in migration has been made repeatedly. What is new are the levels of sophistication of approach to these problems, and the emerging importance of this research in terms of urgent conservation needs. Researchers in North America and Europe are noting rapid, alarming declines in migrant populations. Sound conservation plans will require solid, basic research on migrants, not only on the breeding and wintering grounds, but during migration and at stopover sites as well.

A fascinating area of migration research involves the interplay between physiology, behavior and environment that results in the overt behaviors exhibited by migrants. Frank Moore will present a paper on stopover biology and behavioral responses to energy demand. Many migrants are faced with meeting drastically changing environments along their migratory routes. As Frank will show, some species meet the demands of a changing, unpredictable environment by becoming plastic in their foraging behavior and habitat selection during migration. These behavioral adjustments are the result of constant fine-tuning between internal physiological condition and environmental stimuli. Research concerning how migrants cope with unpredictable and changing environments is not only relevant to basic theory in behavioral ecology, but also has broad implications for conservation.

A very pressing question that is highly relevant to all aspects of migration research is: what are the costs and benefits of distance migration? Piersma and his colleagues have selected the Red Knot to address this question. It would be difficult to choose a more ideal species for this endeavor. Red Knot populations breed at similar latitudes, but migrate vastly different distances to population-specific wintering areas. They successfully examine this question using an energetics approach.

The strategies migrants use to cross major ecological barriers is another topic of current interest. How birds cope with these barriers has been largely the realm of theory.

Biebach and others have recently begun to examine empirically strategies for crossing the Sahara Desert. He finds that a fascinating mix of physiological, behavioral and meteorological variables interact to determine the success, or failure, of a migrant traversing the Sahara.

Peter Berthold's paper is, as far as I am aware, an entirely novel attempt to address the large-scale effects of global warming on migrant populations. Berthold provides specific, testable predictions concerning the effects of global warming on Palearctic migrants. His predictions do not bode well for temperate breeding migrant populations in general. The effects of global warming, use of pesticides and other environmental toxins, and massive habitat destruction may mean the extinction of some migrant populations within the next few decades. The importance of this research cannot be overstated, and Peter's population-level approach is a good starting point.

FOOD AVAILABILITY, FAT DEPOSITION, AND MIGRATORY BEHAVIOUR IN SHORT-DISTANCE VERSUS LONG-DISTANCE MIGRANT *SYLVIA* WARBLERS

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ABSTRACT. It is well established that the migratory behaviour of many species of *Sylvia* warblers is strongly determined by endogenous factors. These factors determine, to a large extent, the timing, distance and direction of migration. Recent experiments, however, indicate that there is considerable plasticity in the system. Of particular interest are the relative roles of endogenous and exogenous factors in producing overt migratory behaviour in a variable environment. This paper reports on experiments performed on Blackcaps *Sylvia atricapilla*, a short-distance migrant, and Garden Warblers *Sylvia borin*, a long-distance migrant. These experiments were designed to test the effects of various levels of food deprivation on fat deposition and migratory behaviour during the autumn and winter months. The results indicate substantial differences, as well as close similarities, in ecophysiological and behavioural strategies in these two closely related migrants. The results are discussed with respect to the different environments these warblers encounter during the autumn migration and winter months.

ECOPHYSIOLOGICAL AND BEHAVIORAL RESPONSE TO ENERGY DEMAND DURING MIGRATION

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ABSTRACT. Acquiring enough food to meet energetic requirements is an important constraint during migration. Yet, passage migrants must cope with increased energy demand coupled with environmental circumstances that decrease the certainty that demand will be met. Migrants should experience selective pressure to diversify their foraging behavior (behavioral plasticity), thereby increasing the likelihood that energetic requirements will be satisfied and en route contingencies met. Birds that replenish depleted reserves rapidly improve their chances of a successful migration. When the rate of gain (g/d) among Wood Thrushes and Veerys was examined in relation to arrival mass following a flight across the Gulf of Mexico, fat-depleted birds gained mass more rapidly than birds carrying unmobilized reserves. Red-eyed Vireos, too, apparently compensated for increased energy demand and were more likely to gain mass than fatter birds. Foraging observations of Red-eyed Vireos were consistent with the hypothesis that lean individuals adjusted their foraging behavior to mediate compensatory weight increase. As energy demand is satisfied, foraging "decisions" can be expected to change.

Keywords: Migration, energetics, Gulf of Mexico, foraging behavior, plasticity.

INTRODUCTION

Behavioral plasticity among long-distance migrants should come as little surprise given the different vegetation structures, wide variations in resource quality and quantity, and changes in competitive pressures experienced during their annual cycle (see Keast & Morton 1980, Hutto 1985). Morse (1971, 1980, see also Rabenold 1980, Greenberg 1990, Loria & Moore 1990, Martin & Karr 1990) suggested that the contingencies which arise during migration place a premium upon plasticity, which is defined here as the ability of an organism to alter its behavior in response to changes in environmental conditions. While en route, a passage migrant must forage in unfamiliar habitats to replenish depleted energy stores, resolve conflicting demands of predator avoidance and food acquisition, compete with other migrants and resident birds for limiting resources, respond to unpredictable and sometimes unfavorable weather, and correct for orientation errors. Moreover, favorable en route habitat, where the bird can safely and rapidly accumulate energy reserves, is probably limited, or effectively so because it may not always have the opportunity to select the best habitats (Hutto 1985, Moore & Simons in press). These "problems" are magnified because the certainty with which contingencies will be met decreases while en route (see Alerstam 1978, Buskirk 1980, Sandberg et al. 1988, Moore & Kerlinger 1991).

In this paper, I consider the adaptive value of foraging plasticity in the context of stopover biology and suggest that migrants diversify their foraging behavior (*sensu* Real 1980) under conditions of high energy demand, thereby increasing the likelihood they will satisfy energetic requirements and meet en route contingencies. How well migratory birds respond to the energy demands of migration affects their survival and

reproductive success. Although it is difficult to measure directly the effect of en route foraging events on survival or reproductive success, rate of fat deposition represents a suitable fitness surrogate to evaluate the functional consequences of foraging behavior during migration. As energy reserves are mobilized during migration, birds that replenish reserves rapidly improve their chances of a successful migration (Alerstam & Lindstrom 1990).

When birds arrive along the northern coast of the Gulf of Mexico, for example, some individuals have mobilized their lipid reserves, are essentially fat-free, and run the risk of a negative energy balance, while others have retained sufficient fat to continue migrating the day of their arrival (e.g., Rappole & Warner 1976, Moore & Kerlinger 1987). Even if a lean migrant achieves a positive energy balance, field studies reveal that lean birds often stay longer during stopover than fatter birds, presumably to replenish depleted energy reserves (Bairlein 1985, Biebach et al. 1986, Moore & Kerlinger 1987, Safriel & Lavee 1988). One consequence of a longer stopover would be delayed arrival on the breeding grounds and lost breeding opportunities (cf. von Haartman 1968, Francis & Cooke 1986, Lavee & Safriel 1989). It is reasonable then to expect the evolution of compensatory mechanisms in migrant populations to meet nutritional demands and to prevent delays in the migratory schedule. If energetically constrained migrants increased their rate of energy acquisition, a favorable energy budget is achieved more quickly, length of stopover decreases, and the speed of migration increases (see Alerstam & Lindstrom 1990). Is there evidence that neotropical landbird migrants make compensatory adjustments in relation to the energy demand experienced during migration? If so, are the adjustments mediated by diversification of foraging behavior?

METHODS

The data reported here on the biology of Wood Thrushes *Hylocichla mustelina*, Veerys *Catharus fuscescens*, and Red-eyed Vireos *Vireo olivaceus* were collected when birds stopped following spring trans-Gulf migration at a coastal woodland located in Cameron Parish, Louisiana, USA (see Moore & Kerlinger 1987, Loria & Moore 1990). The woodlands and wooded islands along the northern coast of the Gulf of Mexico are important stopover sites for neotropical landbird migrants (Moore et al. 1990, Moore & Simons in press). These habitats provide spring migrants a place to rest and replenish reserves following a nonstop, trans-Gulf flight (18-24 h) of at least 1000 km.

Mist-nets (12 x 2.6 m with 30 mm mesh) were used to capture migrants during stopover in 1986 (10-21 April), 1987 (1-28 April), and 1988 (26 March-14 May). Birds were weighed to the nearest 0.25 g, fat classed (see Helms & Drury 1960), banded with a USFWS aluminum leg band, and their wing chord (unflattened) measured. Recaptured birds were assigned to a fat class without reference to previous records and body mass remeasured. I assume that size-adjusted ($\text{mass} \div \text{chord}$) changes in mass between initial capture and recapture represent changes in stored body fat.

Duration of stopover and rate of mass change were estimated by analyzing recapture data. Stopover length was conservatively calculated by subtracting the first capture date from the last capture date (Moore & Kerlinger 1987). I assume that the absence of recapture is indicative of departure from the stopover site (e.g., Bairlein 1985,

Biebach, et al. 1986, Rappole & Warner, 1976, Safriel & Lavee 1988). The daily rate of mass change was computed by dividing the change in mass between first capture and last capture by the duration of stopover. I standardized the daily rate of mass change by computing the percent change/h for individuals recaptured on the same day (Moore & Kerlinger 1987, Loria & Moore 1990). The %/h rates were used to correct masses to 12:00 h for all birds that were recaptured and to control for diurnal variation in mass due to food consumption.

The foraging behavior of Red-eyed Vireos in relation to energy demand was quantified by taking advantage of naturally occurring variability in the arrival condition of birds following trans-Gulf migration in spring (see Moore & Kerlinger 1987, Loria & Moore 1990). Foraging observations were made independent of mass and energy reserve estimates, i.e., an energetic condition ("lean" vs. "fat") was assigned to a foraging bird based upon the average condition of birds captured on a particular day after foraging data were gathered (see Loria & Moore 1990). Fat-free mass in this species is reported to be 14.6 g for females and 15.1 g for males according to Connell et al. (1960), and birds classified as lean (fat score = 0) following trans-Gulf flight averaged 14.3g, regardless of sex. The difference between the average adjusted masses under these two situations translates to approximately 450 km flight-distance under no-wind conditions (Pennycuick 1969).

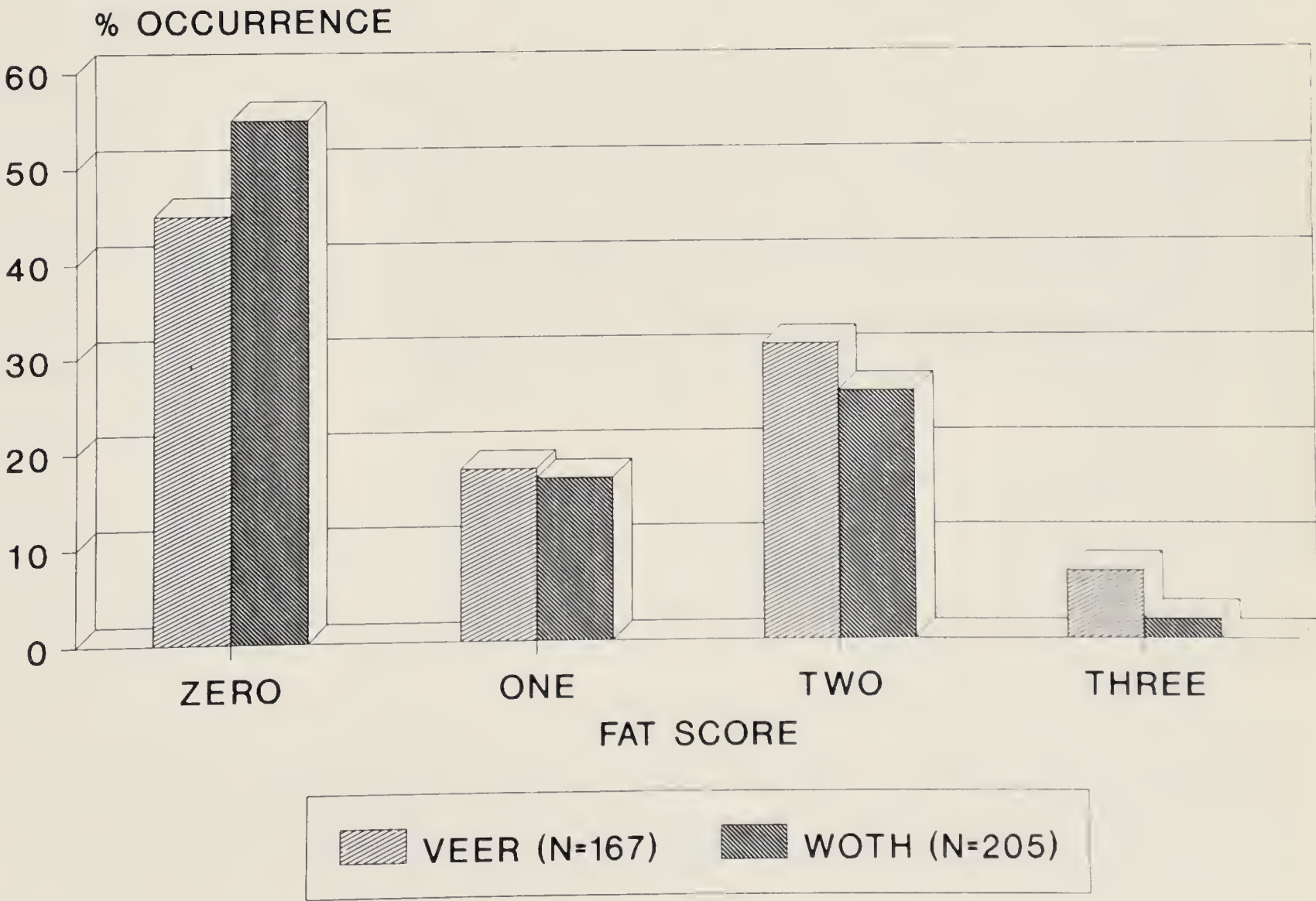


FIGURE 1 – Distribution of fat scores for Wood Thrushes (WOTH) and Veerys (VEER) captured along the northern coast of the Gulf of Mexico in spring 1988. Fat scoring after Helms & Drury (1960). See text for relationship between fat score and body mass.

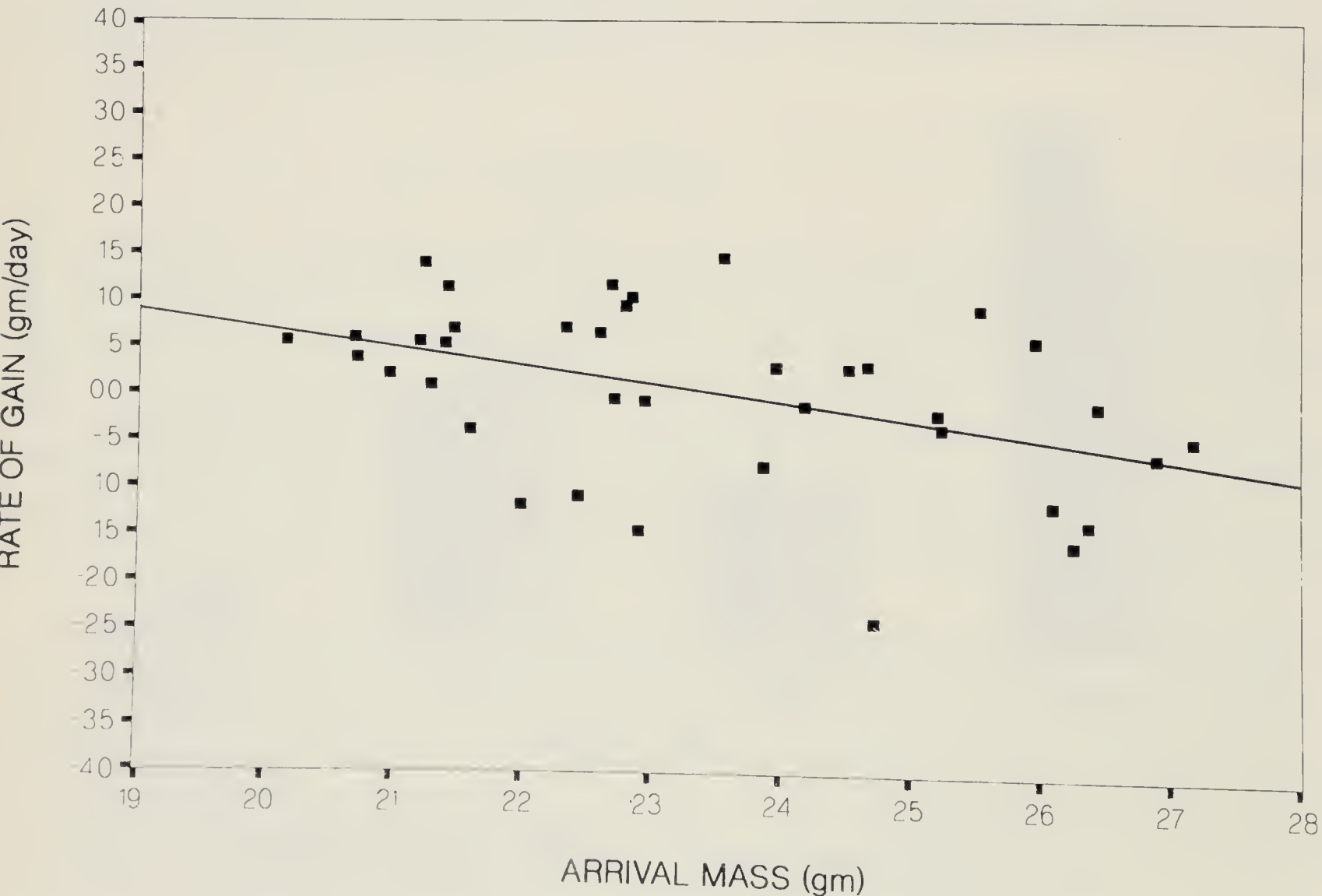
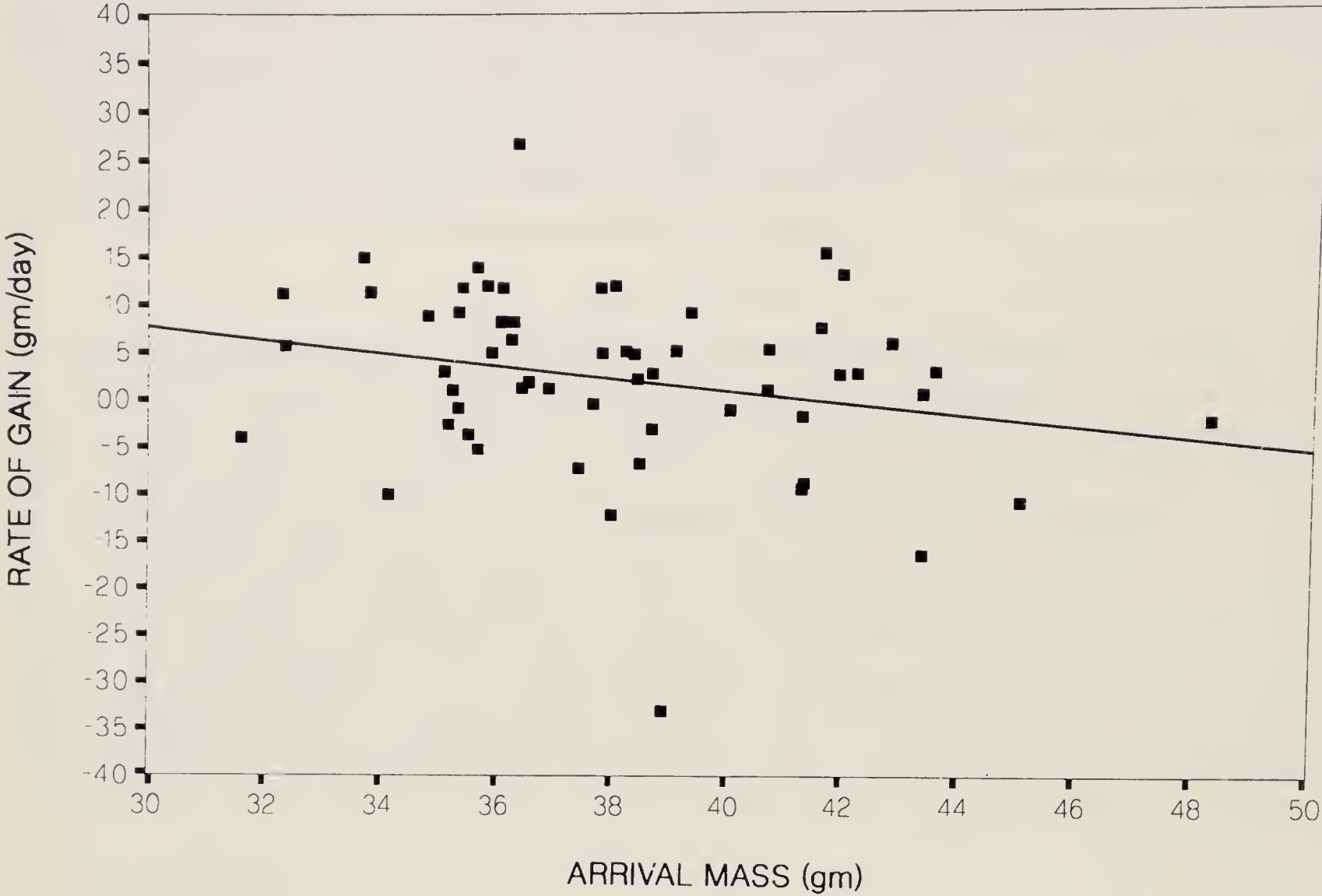


FIGURE 2 – Relationship between rate of mass change and arrival mass of Wood Thrushes (top) and Veerys (bottom). Line is simple linear regression fitted by least squares analysis. The regression line has a significantly negative slope ($P < 0.05$) for both species.

RESULTS & DISCUSSION

Arrival condition and mass change among thrushes

Migrants would be expected to mobilize fat reserves when crossing the Gulf of Mexico in spring, and half of all Veerys and Wood Thrushes captured in 1988 were essentially fat-free (Figure 1). Yet, over one-third of the birds carried reserves greater than or equal to the amount for fat class 2, which is enough "fuel" to continue migrating well beyond the northern Gulf coast. The difference in body mass of Wood Thrushes and Veerys given fat class 0 and those given fat class 2 is 4.1 g and 3.5 g, respectively. This difference translates approximately to flight distances under still-air conditions of 430 km and 570 km, respectively (Pennycuick 1969), and could represent a substantial "savings" in time of migration (see Alerstam & Lindstrom 1990).

If lean, fat-depleted thrushes compensate for heightened energy demand, they should gain mass more rapidly during stopover than birds carrying unmobilized reserves. When rate of gain (g/d) is regressed against arrival mass (Figure 2), the slope of the best fit line is negative ($P < 0.05$) for both species. Lean Wood Thrushes and Veerys gain mass more rapidly than fatter contemporaries, though only a fraction of the total variation in rate of gain is explained by arrival mass ($r^2 = 6\%$ and 19% , respectively). Low coefficients of determination are not surprising given the different variables that probably influence rates of mass change during stopover (Rappole & Warner 1976, Mehlum 1983, Bairlein 1985, Biebach et al. 1986, Moore & Kerlinger 1987, Safriel & Lavee 1988).

Changes in Foraging Behavior of Red-eyed Vireos

When Red-eyed Vireos stopover at Peveto Woods following trans-Gulf migration, some individuals gain mass at a rapid rate, others lose mass, and many birds maintain their arrival mass (Loria & Moore 1990). Some of the variation in rate of mass change is explained by the birds' energetic condition. For example, fatter birds (fat score > 1) lost more mass on a daily basis than did lean birds (fat score = 0) in 1988. Like Wood Thrushes and Veerys, Red-eyed Vireos apparently compensated for increased energy demand and were more likely to gain mass than fatter birds (Loria & Moore 1990).

Loria and Moore (1990) hypothesized that lean Red-eyed Vireos adjusted their foraging behavior to compensate for increased energy demand. They found that fat-depleted birds (1) moved at a higher mean velocity, (2) increased their degree of turning following a feeding attempt, (3) broadened their use of microhabitat space, and (4) expanded their feeding repertoire (Figure 3). The behavior of fat-depleted Red-eyed Vireos following trans-Gulf migration, notably their increased use of space and expanded repertoire, is indicative of risk taking in relation to increased energy requirements (see Real & Caraco 1986, Moore & Simm 1986), i.e., the birds were responding to an anticipated decrease in expected gain. As a consequence of behavioral adjustments, a lean bird increased the likelihood it would gain mass. As energy demands are satisfied and the deficit reduced, foraging "decisions" can be expected to change (see Sibley & McFarland 1976, Houston & McNamara 1982).

Uncertainty and Plasticity Among Passage Migrants

Two conditions lead to plasticity: (1) Predictable periods of trophic constraint and (2) unpredictable but probable periods of trophic constraint. Both criteria are fulfilled dur-

ing migration: passage migrants can anticipate increased energy demand, and they experience increased uncertainty that energy demands will be met (e.g., Rappole & Warner 1976, Graber & Graber 1983, Loria & Moore 1990, Martin & Karr 1990, Moore & Simons in press). The expectation that foraging plasticity is advantageous in relation to energetic constraints may be derived from Real's (1980) consideration of the diversification of behavior in relation to environmental uncertainty. According to Real's model, every behavior will have associated with it some form of probability distribution around its expected value and resulting fitness. The variance of this distribution is essentially the uncertainty that any given behavior will actually result in the expected fitness. While en route between breeding and wintering areas, migrants are required to make "decisions" when outcomes are difficult to ascertain. Assuming that increased expected fitness is desirable and increased uncertainty about that fitness is undesirable, an uncertain strategy will be adopted only if the activity is compensated by an increased expected fitness. Real (1980) shows that under most conditions strategies composed of a variety of behaviors prove to be most advantageous (i.e., organisms try to minimize the uncertainty associated with outcomes), and hypothesizes that when fitness is uncertain an organism's best strategy consists of a diversity of behaviors whose covariances are negative. Expanding feeding repertoire to satisfy energy demand would be most advantageous when the "rewards" associated with different maneuvers negatively covary.

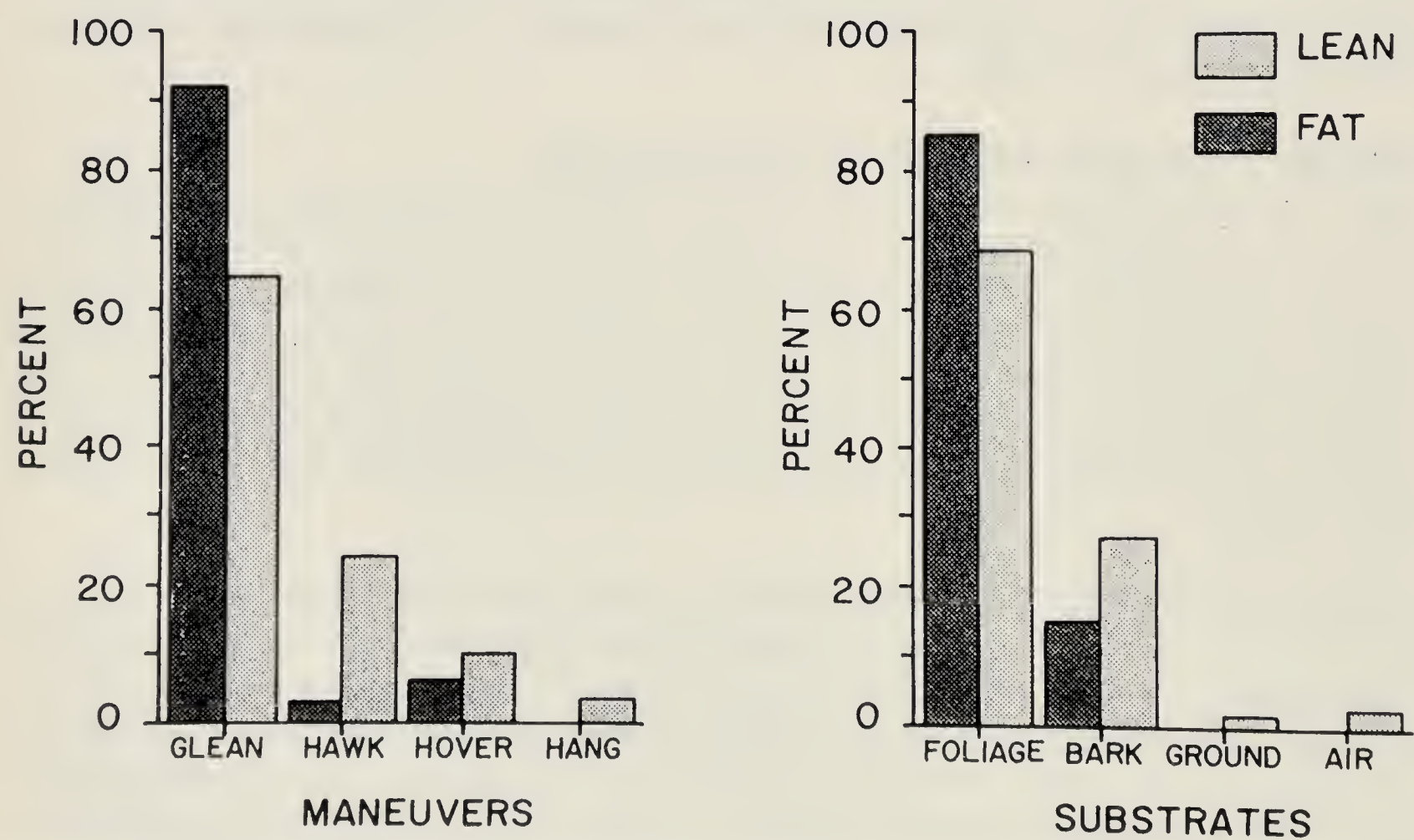


FIGURE 3 – Occurrence (%) of foraging maneuvers (left) and substrates (right) in relation to the energetic condition of Red-eyed Vireos following spring trans-Gulf migration. Maneuvers: N = 117 (lean) and 94 (fat). Substrates: N = 89 (lean) and 117 (fat). Drawing from Loria & Moore (1990).

Altering foraging behavior to meet en route contingencies is not without costs, however. Certain maneuvers are energetically more expensive to perform than others (e.g., Norberg 1977), may expose the forager to increased risk of predation, or may be difficult to perform because of morphological constraints (e.g., Moermond 1990). Yet, when a bird's energy deficit is large, altering foraging behavior to reduce the

deficit becomes worthwhile because a change in the deficit substantially reduces the cost of changing behavior. As energy demand is met and the deficit reduced, however, the cost of changing behavior is less offset (Sibley & McFarland 1976). The en route ecology of migratory birds is profitably viewed as a dynamic interaction between possible behavioral actions and a changing internal state.

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TEMPERATE VERSUS TROPICAL WINTERING IN THE WORLD'S NORTHERNMOST BREEDER, THE KNOT: METABOLIC SCOPE AND RESOURCE LEVELS RESTRICT SUBSPECIFIC OPTIONS

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ABSTRACT. The breeding of Knots *Calidris canutus* is confined to the tundra areas around the Arctic Ocean. The four recognized subspecies winter at latitudes varying from north temperate Europe and N.America to tropical W.Africa, southernmost S.America and New Zealand. Their arctic breeding leads to high thermostatic requirements and hence to a high level of energy expenditure during the summer season. In the non-breeding season, thermostatic costs remain at the same high summer level in the north temperate wintering subspecies, but are halved in the tropical winterers. The considerable difference in overall energy expenditure in winter appears reflected in subspecific Basal Metabolic Rates measured in midwinter, suggesting that metabolic scope and evaporative water loss have been adjusted in the course of evolution to the tropical winter quarters as an adaptive response. Although saving on thermostatic costs, the tropical winterers face energetic bottlenecks during spring migration. Preliminary calculations suggest that wind assistance is essential to balance their migratory budgets. This finding may be more generally applicable to the problem of the origin of migratory pathways.

Keywords: Migration, Knot, *Calidris canutus*, metabolism, thermoregulation, energetics, BMR, subspecific variation, food resources, travel costs, wind effects.

INTRODUCTION

Frozen and covered under snow for more than nine months of the year, the sparsely vegetated land around the Arctic Ocean becomes teeming with bird life during the short Arctic summer. Most species annually exploiting this vast temporarily productive habitat, winter in the far south, and the Knot *Calidris canutus* is a typical example of such an extreme longdistance migrant. During the non-reproductive season, Knots roam along the edges of all continents, in the few wildernesses with a sufficient area of intertidal flats still extant. At this season they usually occur in large flocks and depend on small benthic shellfish for food.

Knots, with a circumpolar but discontinuous distribution, only breed on high Arctic tundra, usually north of the Arctic Circle and north of the 10°C July isotherm (Figure 1 left). Four subspecies are currently recognized. Two subspecies occur in W. Europe. They breed in N.E. Canada and Greenland (*C.c.islandica*) and in the Taymyr Peninsula region in Siberia (*C.c.canutus*) (Figure 1 right), and will be the focus of this contribution. The *islandica* subspecies winters in a few large estuaries in N.W. Europe (50-55°N). During their migrations to and from N. Greenland and N.E. Canada the birds stop-over in Iceland and in N. Norway (Davidson & Wilson 1991). The *canutus* subspecies winters in W.Africa (10-20°N), the majority of birds frequenting two coastal sites, the Banc d'Arguin in Mauritania and the Archipelago dos Bijagos in Guinea-Bissau (Smit & Piersma 1989). The Wadden Sea is their main stopover site during both northward and southward migrations (Dick et al. 1976, 1987, Piersma et al. 1991).

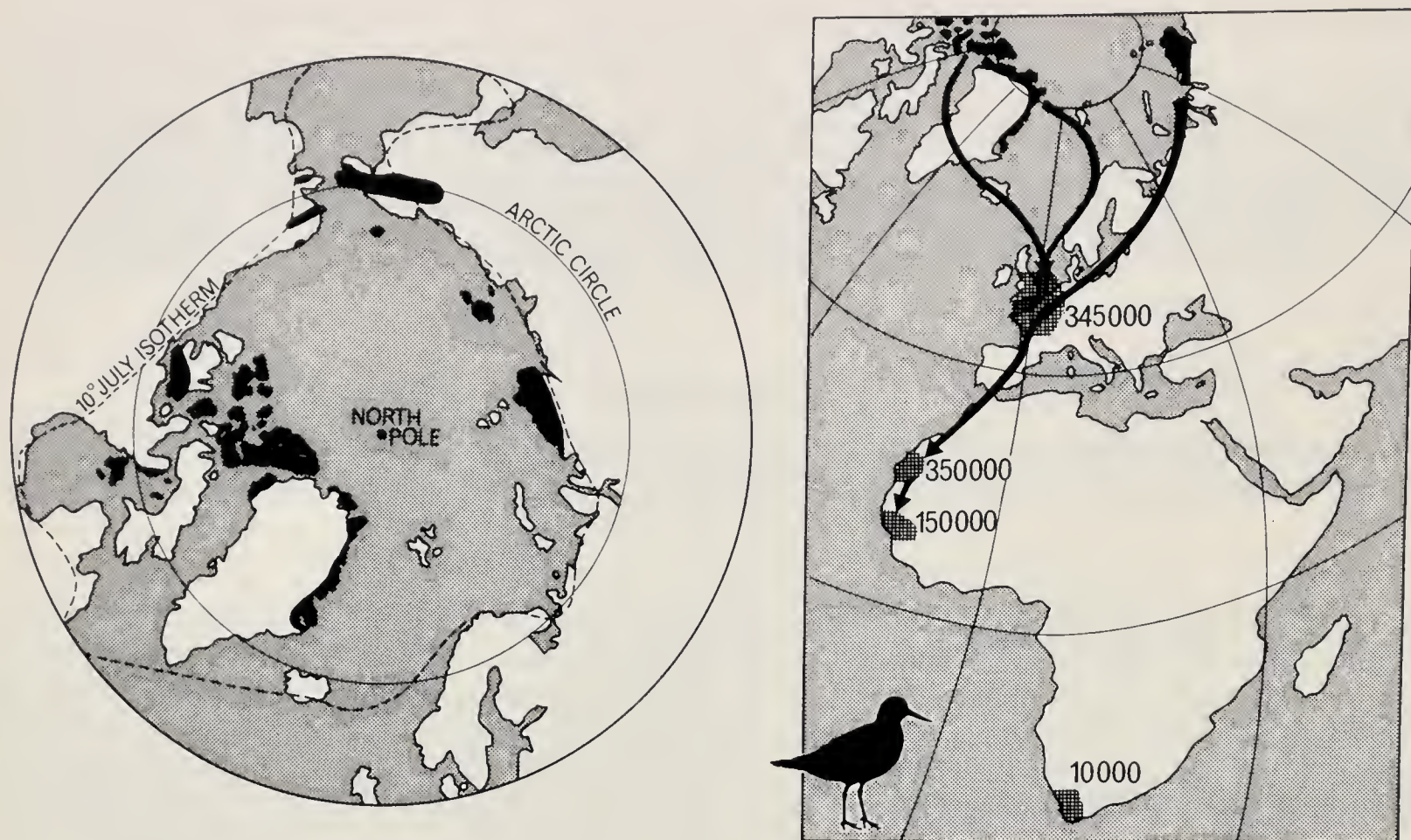


FIGURE 1 - Circumpolar breeding distribution of Knots (adapted from Tomkovich 1991), the map also showing the 10°C isotherm (from Stonehouse 1989). At right the migration patterns of the *canutus* subspecies breeding in Siberia and wintering in W. Africa, and the *islandica* subspecies breeding in Greenland and N.E. Canada and wintering in W. Europe are shown. The figures indicate population sizes at the main wintering sites (from Smit & Piersma 1989).

A first step in ecologically evaluating the within-species variation in wintering latitude, is logically the analysis of the energetic repercussions associated with such differences (Myers et al. 1985, Castro 1988, Summers et al. 1989, Drent & Piersma 1990). Breeding in the high Arctic, a relatively cold and windy region of the world, is likely to entail a considerable cost to uphold endothermy in waders, since they are not particularly well insulated (Kersten & Piersma 1987). We expect these “thermostatic costs” to weigh heavily in the energy budgets of such high Arctic breeders. In winter, the birds might save on thermostatic costs by moving south, but would incur higher travel costs the further south they go (Drent & Piersma 1990). In this contribution we present an empirical assessment of the thermostatic costs of Knots on their Arctic breeding grounds in N.E. Canada, and explore how much cheaper life is likely to be on the more southerly wintering grounds. A further element in this assessment is the estimation of migratory cost from information on mass changes, and novel is the finding that travel costs differ greatly depending on the route followed. These new viewpoints define costs and benefits of current latitudinal range differences and allow speculation on how the spectacular differences in wintering area in Knots are likely to have come about.

METHODS

Fieldwork on wintering Knots was carried out on the Banc d’Arguin in Mauritania and in the Dutch Wadden Sea, and on Knots during the breeding season in Arctic Canada. At each of these sites the activity patterns, feeding behaviour and presence in different microhabitats was studied. To approximate the thermostatic costs of live birds in

the field, we have chosen to use the approach of "heated taxidermic mounts", developed and advocated by G.S. Bakken and coworkers (Bakken 1976, 1980, Bakken et al. 1981, 1985, P. Wiersma & T. Piersma in prep.). Such "copper Knots" mimic a static bird in its environment as well as its thermoregulatory response (i.e. an increasing metabolism). The heated taxidermic mount used in this study is a hollow copper model of a skinned body covered by a fresh, prepared and complete skin of a Knot, which is mounted in a natural standing position (see Figure 2 bottom). A thermistor inside the model is connected to a thermostat which can be set to keep the internal temperature of the model at the natural constant of 41°C, the required heat being generated by a heating wire embedded in the copper model's wall. In this way the combined effects of air temperature, wind and radiation, as they affect Knots in different microhabitats, can be measured in an integrated way. The power consumption of the heated taxidermic mounts was calibrated under standardized laboratory conditions (either a pitch black plexiglass respiration box without wind, or a darkened small windtunnel with a wind force of 1 m/s) over a range of temperatures to the metabolism of live Knots determined from O₂-consumption as measured under exactly the same conditions. The methodology of the O₂-consumption measurements is described by Kersten & Piersma (1987), with the difference that in this study only values from night-long continuous measurements of post-absorptive resting metabolism under constant conditions were used. It was reassuring that calibrations of heated models to live birds under both wind-free and wind conditions (situations of free and forced convection, respectively) led to the same estimated thermostatic costs under these conditions. The Knots used in these experiments were captured in the Dutch Wadden Sea in winter, and had been in captivity under the normal Dutch photoperiodic regime for 1.5 years, showing the moult and body mass cycles known from the field as normal (W. Teunissen & T. Piersma in prep.; see Kersten & Piersma 1987).

Thermostatic cost is defined as the metabolic rate of birds resting or sleeping in different microhabitats, thus including the basal metabolic rate (BMR), which represents the thermostatic cost under thermoneutral conditions. Thermostatic cost is hence a shorthand for the residual component of the daily energy expenditure excluding activity and energy retention (costs of synthesis), and can be estimated by employing heated taxidermic mounts.

Simultaneously to the measurement of thermostatic costs in different microhabitats in the field, three standard meteorological parameters (dry bulb air temperature, wind speed at heights between 10 and 15 m, global solar radiation) were monitored on a continuous basis at a nearby location. From half-hourly values of both thermostatic cost (=power reading of heated taxidermic mount) and the three meteorological variables measured under a wide range of conditions, simple predictive models to estimate thermostatic costs in different microhabitats from given values of temperature, wind and radiation were derived. In these statistical models (the multiple regressions always explaining more than 95% of the variance in thermostatic costs), the effects of wind and temperature were assumed to be multiplicative, while that of radiation was assumed to be additive (see Bakken 1976, 1980).

Estimates of the field metabolic rate of high Arctic breeding waders in relation to weather conditions, were obtained from a sample of 11 incubating Turnstones *Arenaria interpres*, studied in June-July 1989 on the tundra of Rowley Island, Foxe Basin, Canada (R.I.G. Morrison & T. Piersma in prep.). Field metabolic rates were

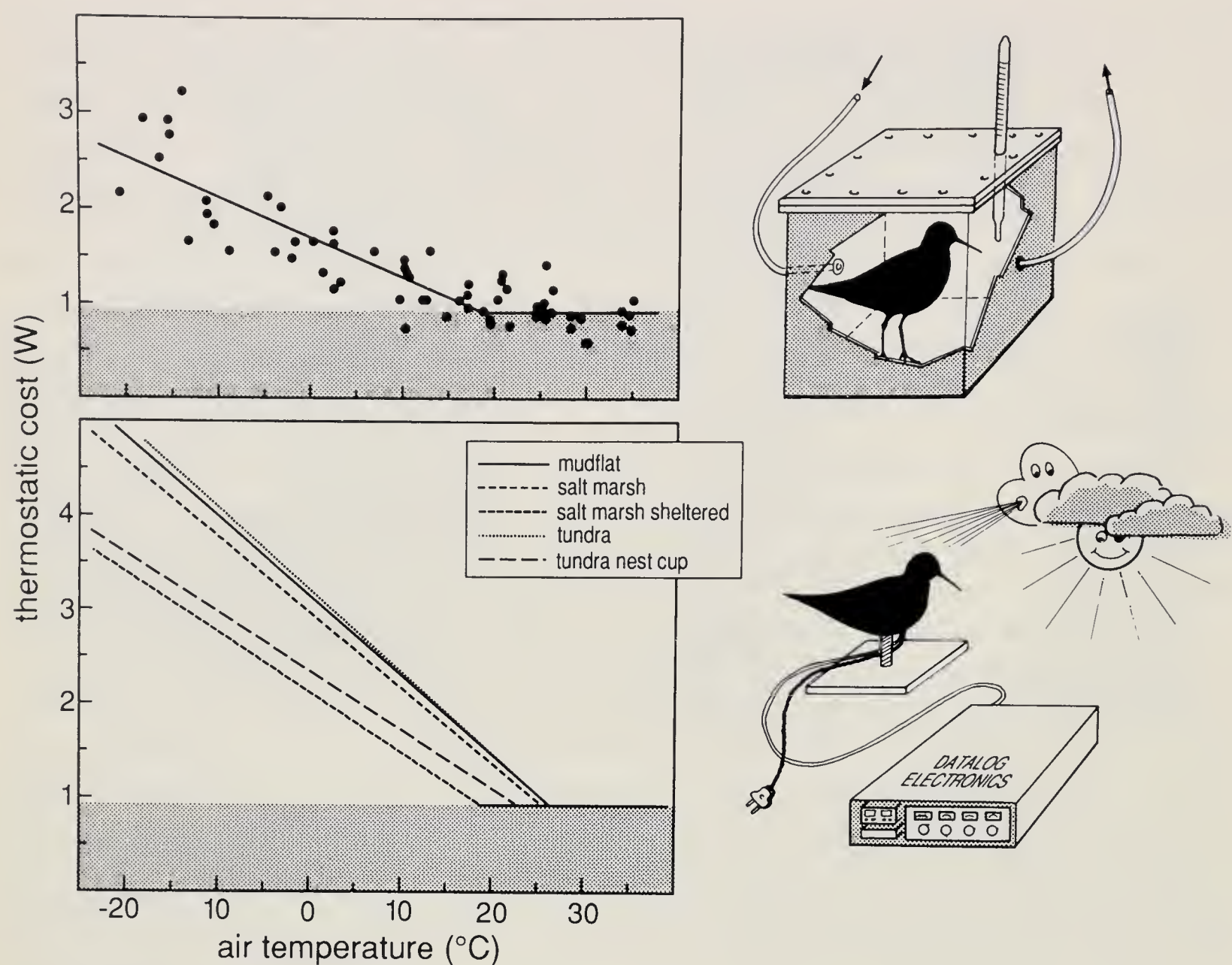


FIGURE 2 - Thermostatic costs of Knots (subspecies *islandica*) under laboratory conditions (top) and in different microhabitats in the field (bottom). For the latter, environmental conditions were standardized as for a cloudy midday with a gentle breeze (3 Beaufort): wind speed is 3 m/s and global solar radiation is 400 W/m². The data in the upper panel refer to night-long continuous O₂ measurements of sleeping Knots in black plexiglass boxes in a climatic chamber, the air temperature reflecting the temperature in the box. The field data are extrapolations of measurements with heated taxidermic Knot-mounts, calibrated in the laboratory to live Knots (see text). In both panels the shaded level indicates the minimum or basal metabolic rate (BMR).

calculated from the turnover rates of doubly-labeled water (D₂O¹⁸). General procedures and methods of analysis followed Masman & Klaassen (1987). Birds were captured on the nest, injected with 2.5 ml doubly-labeled water, kept for 2 hrs after which an initial small blood sample was taken, released and recaptured after 1-4 days to obtain a second blood sample. Simultaneously to these experiments, the thermostatic costs of Knots on the open tundra and in the nest were continuously measured by heated taxidermic mounts. The Turnstone can serve as an acceptable substitute for Knots in view of their taxonomic affinities, equal sizes and body masses, comparable levels of BMR (ca. 1 W in either species, see below and Kersten & Piersma 1987) and the close resemblance of their breeding and feeding habitats in the Arctic.

To obtain a cost factor for each km flown during long distance flights, we have followed a purely empirical approach. Estimates of the loss of fat (with an energy content of 39.3 kJ/g contributing 90% or more to the energy supplied during a long distance flight, Piersma & Jukema 1990) and hence the cost per km flown, could be

derived for four trajectories (data from Davidson & Evans 1986, Dick et al. 1987, Prokosch 1988, Piersma 1989, Piersma & van Brederode 1990, Lindstrom 1990, Morrison & Davidson 1990, Gudmundsson et al. 1991): W. Africa to the Wadden Sea (0.3 kJ/km), Wadden Sea to Taymyr (0.5 kJ/km), S.E. England to N. Norway (0.8 kJ/km), and N. Norway to Ellesmere Island (0.7 kJ/km). For each of these flights there is now ample observational evidence to underpin the interpretation that they are normally traversed in one flight, and not carried out in small hops.

RESULTS

The thermostatic cost curve of Knots of the *islandica* population under defined laboratory conditions is presented in Figure 2 (top). The BMR of these birds amounted 0.95 W, a value which approximates the value of 1 W predicted by Kersten & Piersma (1987) for waders of their mass. Their conductance was $-0.04 \text{ W}/^{\circ}\text{C}$, a value close to the one for the Turnstone as reported by Kersten & Piersma (1987) and the predictions by Kendeigh et al. (1977) and Aschoff (1981) for non-passerine birds at this body mass in winter and in the resting phase of their diurnal cycle, respectively. The relative thermostatic costs of Knots in different microhabitats in the field as measured by the heated taxidermic mounts (Figure 2 bottom), indicate that shelter from the wind (e.g. when roosting between the vegetation on a saltmarsh or when incubating) can considerably reduce thermostatic costs.

The effectiveness of our thermostatic cost estimates to help explain the pattern of energy expenditure of free-living birds, was tested by plotting the field metabolic rate of incubating Turnstones (spending approximately 50% of their time on the nest), to the concurrent thermostatic requirement. The close correspondence in slope (Figure 3) suggests that much of the variation in the field metabolic rate can be explained by compensation for prevailing weather variations. Piersma & Morrison (in prep.) demonstrate that the estimated thermostatic cost factor explains at least 55% of the variation in field metabolic rate. By virtually integrating the combined effects of temperature, wind and radiation, the copper mount data more closely parallel the measured field metabolism than any of the meteorological data sets. Judging from the data displayed in Figure 3, the cost of activity can be estimated at 1-1.5 W. A similarly high level of total energy expenditure (average of 3.5 BMR) is reported for the Purple Sandpiper *Calidris maritima*, studied during the breeding season in high Arctic Spitsbergen by Pierce (1989).

Having shown the utility of the thermostatic cost (as estimated by the heated taxidermic mounts) in explaining the field metabolism of free-living Turnstones, we can now consider the level of thermostatic costs at different locations and seasons. The predictive equations on which Figure 2 (bottom) is based, are used to estimate the thermostatic requirements of Knots living on both tundra and on temperate and tropical mudflats (Figure 4). During the breeding season the cost of living on open tundra is always close to 3 W. If the physiological maximal intake rate estimated by Kirkwood's (1983) allometric equation at 4-5 W, bears relevance to Knots, this leaves little more than 1-1.5 W "energetic leeway" for the costs of activity, i.e. the cost of activity as measured in breeding Turnstones. The Arctic therefore proves to be a costly place to be and breed.

The Knots of the *islandica* subspecies which fly southeast to winter in N.W.Europe face an environment where the average cost of thermoregulation is as high as on the breeding grounds (Figure 4 right): the thermostatic costs when living on the mudflats of the Wadden Sea approximates 3 W. Only Knots which go as far south as W. Africa experience much more congenial weather, and incur thermostatic costs close to 1.5 W, a saving of 50%. This pattern of decreasing field costs with decreasing latitude has been empirically confirmed in free-living Sanderlings *Calidris alba*, studied by Castro (1988) by applying the double-labeled water technique to free-living birds wintering in New Jersey, Texas, Panama and Peru.

Although it is therefore likely that it is metabolically cheaper for Knots to spend the winter in W. Africa than in W. Europe, such birds have to fly much greater distances (Table 1). At present we are unable to empirically estimate all costs associated with these migrations (e.g. variable synthesis costs and working levels, variable costs of transport), but we can roughly compare the costs made during long distance flights (Table 1). In spring, both subspecies cover the distance between wintering and breeding area in two single long flights (Figure 1 right), those of *canutus* being twice as long as those of *islandica* (Table 1). In spite of this, the Siberian breeders leave the wintering and the spring staging area at equal or even lower body masses than the

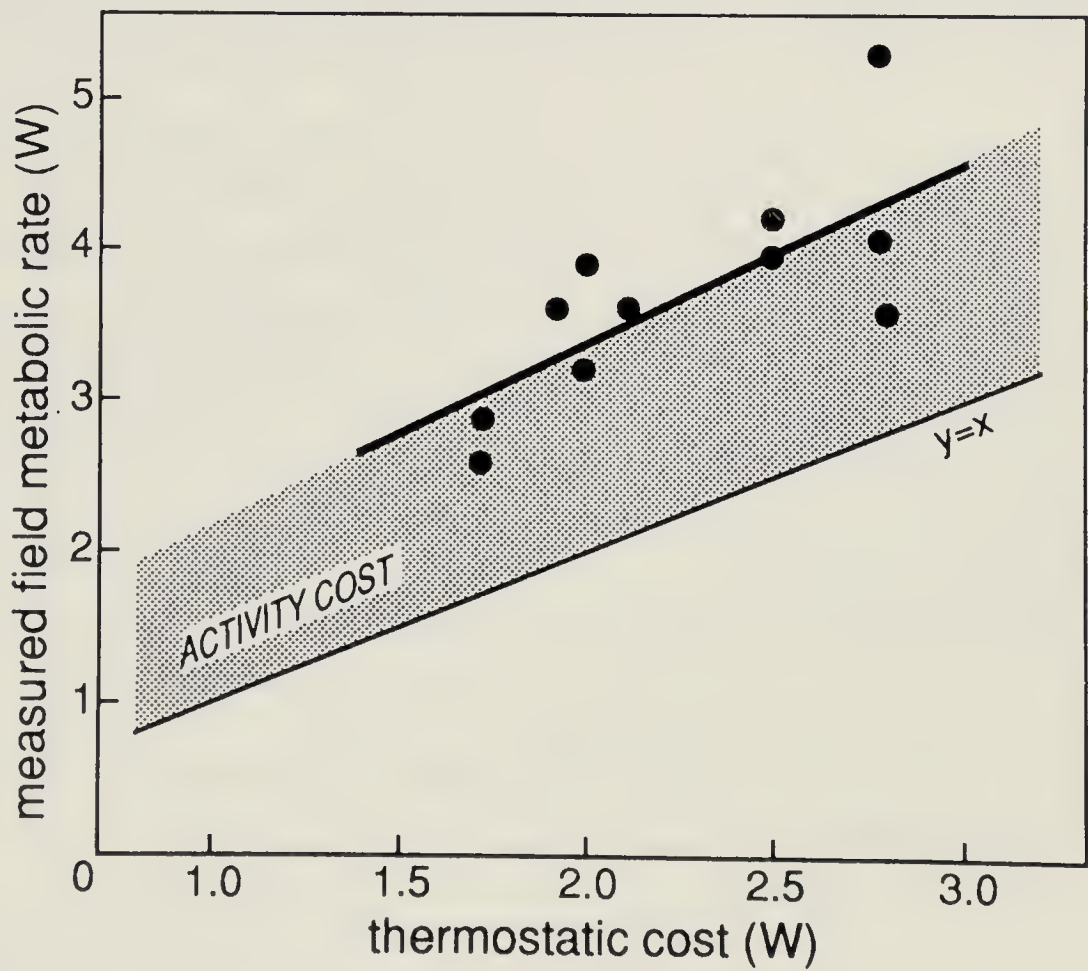


FIGURE 3 - Field metabolic rate of free-living Turnstones in relation to the concurrent thermostatic costs as measured by heated taxidermic Knot-mounts. Field metabolic rate was estimated from D_2O^{18} -turnover measurements in individuals (9 females and 2 males) recaptured at daily or two-daily intervals while halfway through incubation on the tundra of Rowley Island, Foxe Basin, Canada, in early July 1989 (T.Piersma & R.I.G.Morrison in prep.). In the calculation of the average thermostatic cost per experiment, we assumed that the birds spent half of their time on the open ground and the other half in the nest cup (pers.obs.). Field metabolic rate and thermostatic cost are linearly related by the equation: $y= 0.94 + 1.22x$, $r^2=0.55$.

TABLE 1 - Travel distances of, and approximate annual average expenditure on long-distance flights by, a temperate (*islandica*) and a tropical (*canutus*) wintering subspecies of Knot. Cost factors for long-distance flights were calculated from estimated fat losses during specific flight (see methods section). Flight distances were read from a globe and are from Gudmundsson et al. (1991).

Trajectory	Subspecies	
	<i>islandica</i>	<i>canutus</i>
W.Africa - Wadden Sea (km)		4 600
Wadden Sea - Taymyr (km)		4 800
Wadden Sea - Iceland (km)	2 100	
Iceland - Ellesmere Island (km)	2 700	
Total one way (km)	4 800	9 400
Total return (km)	9 600	18 800
Empirical travel cost (kJ/km)	0.7-0.8	0.3-0.5
Annual flight cost (kJ/yr)	6 720-7 680	5 640-9 400
Average cost (W)	0.22-0.25	0.18-0.30

islandica's before a comparable leg of the journey. Therefore, *canutus* ends up with much lower travel costs (this is the cost/km and not the cost/time, the flight cost) than *islandica*. In the particular case of the flight from W.Africa to the Wadden Sea, there are several lines of evidence suggesting that the low cost can be explained by wind assistance obtained by flying at the appropriate altitude (Piersma & Jukema 1990, T.Piersma, P.Prokosch & D.Bredin in prep.). Concerning the journey from the Wadden Sea to Taymyr, Ebbinge (1989) was able to use tailwind as a factor in explaining Siberian Brent *Branta bernicla* breeding success (headwinds in the spring migratory period inhibiting success).

Based on the information assembled on wind patterns by Lamb (1972) we propose that favourable winds account for the low apparent costs during the flight from the Wadden Sea to Taymyr. For each subspecies of Knot the average cost of living on an annual basis is thus increased by 0.2-0.3 W, purely on the basis of net transport cost. At 20-30% of the value of BMR this increment certainly certifies as weighing heavily in the annual energy budgets.

DISCUSSION

Preliminary measurements of BMR in midwinter indicate a correlation between BMR and the inferred winter metabolism (Figure 4) in the two subspecies of Knot examined. The southerly wintering *canutus* has a BMR a factor 0.90 that of the temperate wintering *islandica* (0.10<P<0.05) or a factor 0.78 when expressed per unit mass (W/kg;P<0.05). This confirms the suggestion by Klaassen et al. (1990) that tropically wintering waders might show a lower than predicted BMR. A low BMR as a component of a low overall expenditure may help to reduce evaporative water loss under

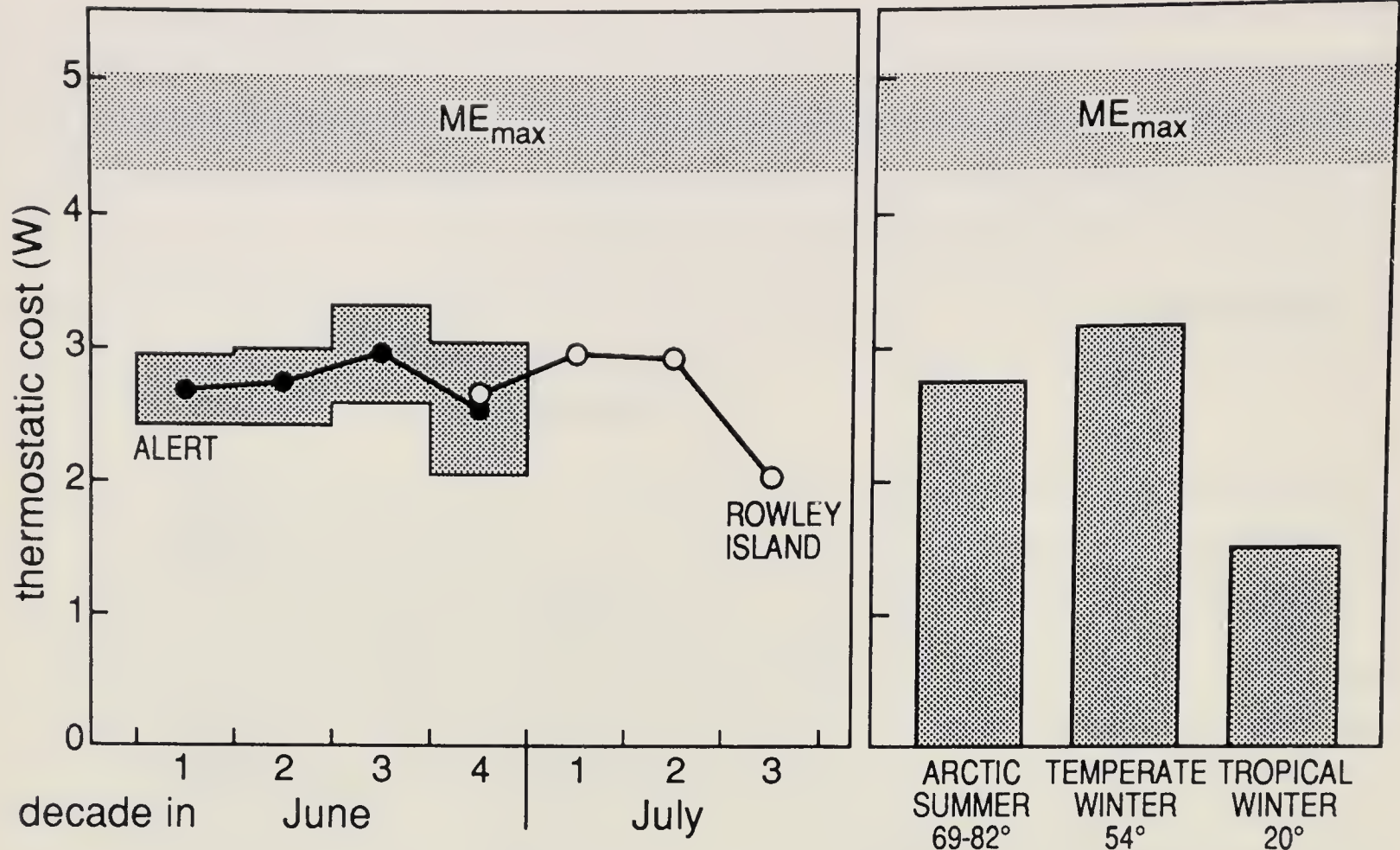


FIGURE 4 - Seasonal changes in the thermostatic costs of Knots standing on the tundra (left), and average thermostatic costs of Knots during the arctic summer (average of weekly values at left), and the temperate and tropical winter on the open mudflats (November through February in the Dutch Wadden Sea and the Mauritanian Banc d'Arguin respectively). At left, closed dots refer to the average conditions in the years 1985-1990 at a high Arctic station (Alert, Ellesmere Island, Canada, 82°N, 62°W), the maximum yearly variation being shown by the shading. The open dots refer to measurements by heated taxidermic mounts on Rowley Island, Foxe Basin, Canada (69°N, 79°W) in June-July 1989 (T.Piersma & R.I.G.Morrison in prep.). For Alert, the Wadden Sea and the Banc d'Arguin the values are estimated from predictive equations relating temperature, wind and solar radiation to the bird's energy requirement and weather data supplied by the Atmospheric Environment Service of Canada, the Dutch Royal Meteorological Institute (KNMI) and Wolff & Smit (1990). The range in maximum metabolizable energy intake rates (ME_{max}), as estimated by the allometric equation of Kirkwood (1983) for birds between 120 g and 150 g, is indicated by the shaded area.

heat stress. Evaporative water loss may provide a physiological constraint to heat production (=work) in birds which can only obtain salt water, either from their prey or from the sea. Although saving water under conditions of heat, a lowered BMR may reduce the metabolic scope (recalling the 'energetic margin hypothesis' of Kersten & Piersma 1987), and thus constrain the work level options open to tropical winterers.

The suggestion of an energetically expensive life by temperate winterers (Drent & Piersma 1990) is confirmed by the data presented in Figure 4. We have elaborated on this picture to show the overwinter and spring change in thermostatic costs at the two locations (Wadden Sea and Banc d'Arguin) and also to add the synthesis-component implicated in energy (fat) accumulation prior to migratory departures (Figure 5). The curve for *islandica* suggests a compensatory replacement of energy intake for thermoregulatory purposes by energy intake for fat accumulation. The *canutus* individuals wintering on the Banc d'Arguin only show a small increase in costs due to synthesis. They take very long to slowly accumulate their fat reserves in spring (Piersma 1989, Zwarts et al. 1990b). Three facts suggest to us that the resource lev-

els on the Banc d'Arguin may make it impossible to gain fat at a faster rate: 1) Knots fed for all the available time during the period of fat accumulation (Zwarts et al. 1990a), 2) rapid fattening is energetically cheapest since the birds then save on transport costs which increase steeply with increasing mass, and 3) *canutus* is able to gain mass much faster elsewhere (e.g. Figure 5, Dick et al. 1987) and is thus not physiologically constrained. Since food abundance in winter is equal or even lower than in spring (Wolff & Smit 1990), we may extend the suggestion of limiting resource levels to the situation in winter and additionally propose that, although the thermostatic costs of wintering on the Banc d'Arguin are low, the energetic margin to meet these costs could scarcely be much higher in view of food limitations on intake rates.

This leads us to propose a set of interconnected hypotheses on how energetic expenditures of Knots wintering at different latitudes restrict the migratory options open to the different subspecies. Temperate wintering Knots of the *islandica* subspecies (with a high BMR) would be unable to winter in the tropics (maintaining their high BMR) for reasons of water limitations. In contrast, the tropically wintering *canutus* have a lower BMR, possibly adjusted to cope with the water constraint. A low BMR implies that *canutus* is limited in its metabolic scope and might thus be unable to sustain the large thermostatic costs characteristic of northerly wintering. Root (1988,1989) has recently modelled wintering costs in migrant passerines of N. America and finds a congruent level of thermostatic cost delimiting the northern boundary of the wintering range, arguing that this cost is indeed limiting present day boundaries (Castro,1989,however

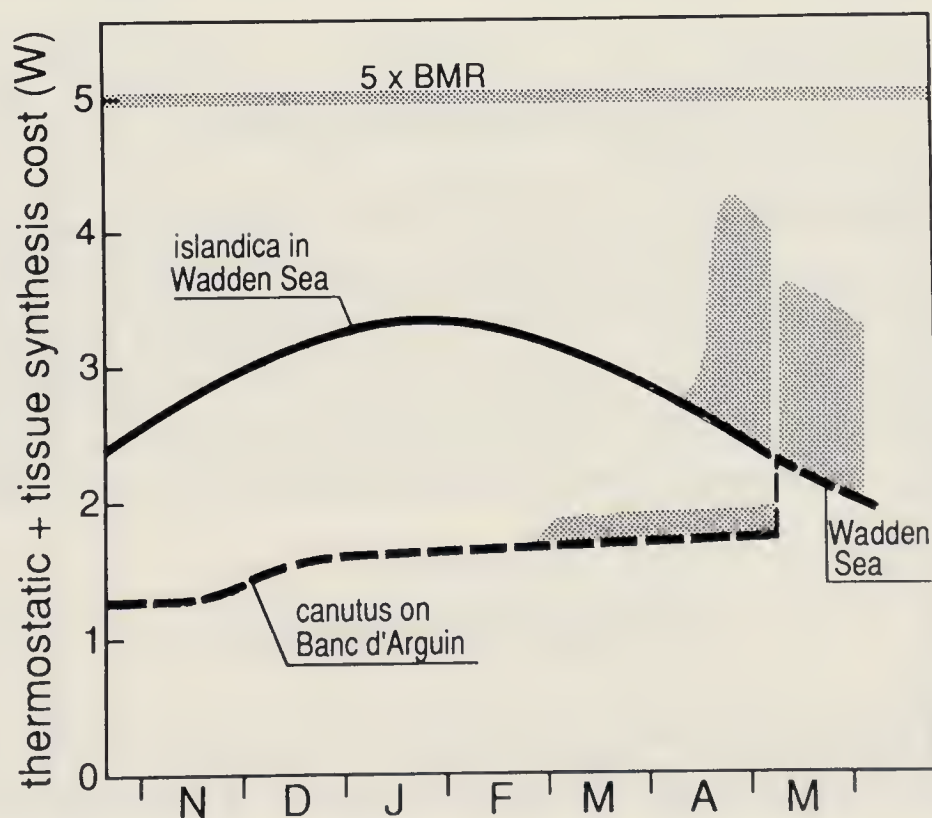


FIGURE 5 - Winter and spring changes of the costs of thermoregulation (thick lines) and tissue synthesis (shaded areas) in two subspecies of Knots: *canutus* wintering on the Banc d'Arguin in Mauritania and migrating via the Wadden Sea to Siberia, and *islandica* wintering in the Wadden Sea and the British Isles and preparing their flight to the stopover sites in Iceland and N. Norway before flying on to northernmost Greenland and Canada. Estimates of thermostatic costs are for birds on open mudflats and are based on predictive equations relating air temperature, wind speed and global solar radiation to thermostatic expenditure as measured by heated taxidermic mounts. The increments in required metabolizable energy intake (which can be considered as a cost) for the synthesis of fat and protein stores are based on the daily mass gains reported by Prokosch (1988) and Piersma (1989), and an estimate of the synthesis cost of body reserve tissue in Knots of 35 kJ/g body mass reported by Klaassen et al. (1990). The line indicates a possible maximum sustained working level of 5 times BMR (cf. Drent & Daan 1980).

taking issue with this conclusion). Although the southerly wintering *canutus* face low, and therefore favourable, daily energy expenditures, they would be unable to sustain higher levels there, in view of the resource limitations imposed by the tropical wintering habitat.

The reported low travel costs of the Siberian-breeding *canutus* are possibly related to predominant wind flow patterns over the west Eurasian continent, which facilitate travel in a SW-NE direction (Lamb 1972). Often one finds almost opposing wind directions at different altitudes up to 10 km (e.g. the trade winds at subtropical latitudes at ground level are matched by the antitrades higher up). It is this bipolar wind axis, that migratory waders can profit from in both seasons. It is tempting to suggest that the Knots from Greenland and N.E. Canada, migrating in a direction perpendicular to this general air flow pattern, have less wind subsidy and thereby end up with higher travel costs. As a corollary to the observation of Alerstam et al. (1986: Figure 20) that the low number of breeding wader species in N.W. Greenland and N.E. Canada may be due to extreme distance to the last suitable staging areas, we hypothesize that the large number of wader species breeding in Siberia (Cramp & Simmons 1983), which is further away than N.E. Canada from the nearest spring staging sites, may be the biogeographical outcome of the predominant air flow patterns over the Eurasian continent. It is clear that we should accept wind assistance as an important resource other than food for migrant waders. We believe that the perspective presented above could open the door to a suite of exciting comparative flyway and weather studies.

FIELDWORKERS ALERT!

Our speculations have made us realize how little observational data bear on the relation between travel costs and prevailing meteorological conditions. We would like to appeal to fieldworkers everywhere to redouble efforts to quantify the mass increases prior to departure, and to include cooperation with biologists at the receiving end of the migration paths in the work. In view of the critical effects of winds on migratory performance, collaboration with meteorologists should increasingly be sought.

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IS WATER OR ENERGY CRUCIAL FOR TRANS-SAHARA MIGRANTS?

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ABSTRACT. For small Passerines crossing the Sahara, two environmental factors, tailwinds and low air temperatures, have been discussed to be critical for the energy and water budget. Fat reserves and water content of unsuccessful, dying birds during migration in the Libyan desert in Egypt were analysed. Whereas the reason for the failure of Swallows *Hirundo rustica* was not obvious, Willow Warblers *Phylloscopus trochilus*, like other small Passerines, ran out of fat, which is the main energy substrate during flight. The water budget was still normal.

Keywords: Trans-Sahara migrants, fat, energy, water budget, dehydration.

INTRODUCTION

Migrants that fly long distances between their breeding and their wintering sites often have to cross ecological barriers such as water, glaciers, mountains or deserts. The number and quality of stopover sites and conditions during flight probably present a greater problem than distance per se to migrants. Each particular ecological barrier poses special problems to migrants depending on the species' characteristics of foraging ecology, flight capabilities and general physiology.

In this paper, I investigate critical factors during migration across the Sahara desert and suggest possible reasons for the failure of some birds undertaking the crossing. Most European birds that winter in tropical Africa have to cross the Sahara with only a minimal probability of finding food or water. Two potential strategies of crossing have been proposed: (1) A non-stop flight over the entire breadth of the desert, a distance of at least 1800 km in autumn (Moreau 1961, 1972) and (2) an intermittent migration with flight during the night and stopover during the day (Biebach et al. 1986). There is no convincing evidence for preferred flights along particular routes such as along the Nile, or along a row of oases in N-S direction in Algeria, or along the West-Atlantic coast (Biebach 1990).

Based on energy and water budget calculations, two conditions during flight have been suggested to be necessary for successful crossing:

- a) First, energy reserves before crossing the Sahara in autumn are, for most birds, sufficient to cross without refuelling only if they experience tailwinds of at least 8 m/s (Biebach 1990).
- b) Second, water balance can only be maintained if the *air temperature* during flight is below 10 °C. Otherwise, the birds would have to regulate their temperatures by evaporation and they would quickly reach critical values of dehydration (Biesel & Nachtigall 1987, Hudson & Bernstein 1981, Torre-Bueno 1978, Tucker 1968, 1974).

These conditions of tailwind and low air temperature cannot be met simultaneously during all days during the autumn migration period. If appropriate tailwinds can be found only at an air layer with temperatures higher than 10°C (normally below 2000 m above ground) the birds cannot balance their water budget. On the other hand, if they choose to fly at an air layer with temperature below 10°C they might confront headwinds and encounter energetic problems. Under these conditions, it has been suggested that birds stop flying and rest until dark, when acceptable temperatures are at lower altitudes where favorable tailwinds prevail. Unfortunately, we currently lack direct measurements of wind and temperature profiles, integrated with studies of stopover behavior of migrants in the Sahara. Based on the hypothesis concerning nonstop versus intermittent migration, we predict that birds stopping over in the desert would have a balanced water budget and sufficient energy reserves to continue the crossing because resting is interpreted as behavior to escape detrimental flight conditions. And, in fact, birds stopping over in the desert generally have the expected normal water budget and energy reserves (Biebach 1988, 1990). On the other hand, many observers reported exhausted, dying or dead migrants in the Sahara. In some cases, it has been obvious that the birds could not escape long-lasting sand storms, but in most cases the reasons for their failure are unknown. Investigation of such birds could shed some light on critical factors during migration. Yapp (1956, 1962) and Fogden (1972) have previously discussed water as a potential limiting factor on migratory range on purely a theoretical basis.

METHODS

I investigated samples of birds found in a small oasis "Sadat Farm" in the Libyan desert in Egypt and in a mountain ridge called "Sposserberg" during autumn migration. Both sites were about 300 km south of the Mediterranean coast and about 200 km west of the Nile (for a detailed description of location and the habitat see Biebach et al. in prep). Two groups of mist-netted birds were investigated for their water and fat content: two samples of 18 "normal" Willow Warblers *Phylloscopus trochilus* and 10 "normal" Lesser Whitethroats *Sylvia curruca*. "Normal" means the birds have been caught with mistnets out of a pool of birds with the normal escape behavior. The second group of birds investigated were obviously close to death because they were sitting on the ground with fluffed feathers and were caught by hand. Eight Swallows *Hirundo rustica* and two Willow Warblers were analysed. Birds were collected primarily in the morning, shortly after arrival at the stopover place. Thus the condition of the dying birds were mainly caused by migratory flight.

Immediately after capture the birds were weighed to the nearest 0.1 g and deepfrozen for later analysis. In the laboratory the birds were then dried at 60°C to constant mass. The difference between fresh mass and dry mass was the water content. Fat was extracted with petroleum-ether in a Soxhlet apparatus. The extracted fat was directly weighted and the remaining material dried to constant mass was the lean dry mass. Water and fat were expressed as percent of lean dry mass.

Several problems arise for the interpretation of the water budget. First, we want to know at what point of dehydration birds can no longer maintain basic physiological functions like temperature regulation or heart rate, and second, how one can predict how close a dehydrated bird is to this point. The water content of hydrated birds is

regulated within a narrow range (Odum et al. 1964); when expressed as % water of total body mass it is close to 66 %. Homeostatic water balance is maintained irrespective of fat storage, thus the water content is expressed as % water of the fat-free dry mass or lean dry mass. This index is normally at about 220 for hydrated birds and birds with values below 200 are regarded as dehydrated (Fogden 1972). Desert birds and probably small passerine migrants can tolerate dehydration down to about a water index of 150 (Skadhauge 1974,1981, Fogden 1972).

RESULTS

Two groups of 18 Willow Warblers and 10 Lesser Whitethroats, regarded as representative samples of birds normally stopping in the Libyan desert, had a mean water index of 209 ± 22 (SD) and 237 ± 26 (SD) respectively and both indices were very similar to a sample of 808 birds from nine species that had been killed during autumn migration at a television tower in North America with values between 204 and 225 (Child & Marshall 1970). One bird from the Willow Warbler sample had a water index of 149,

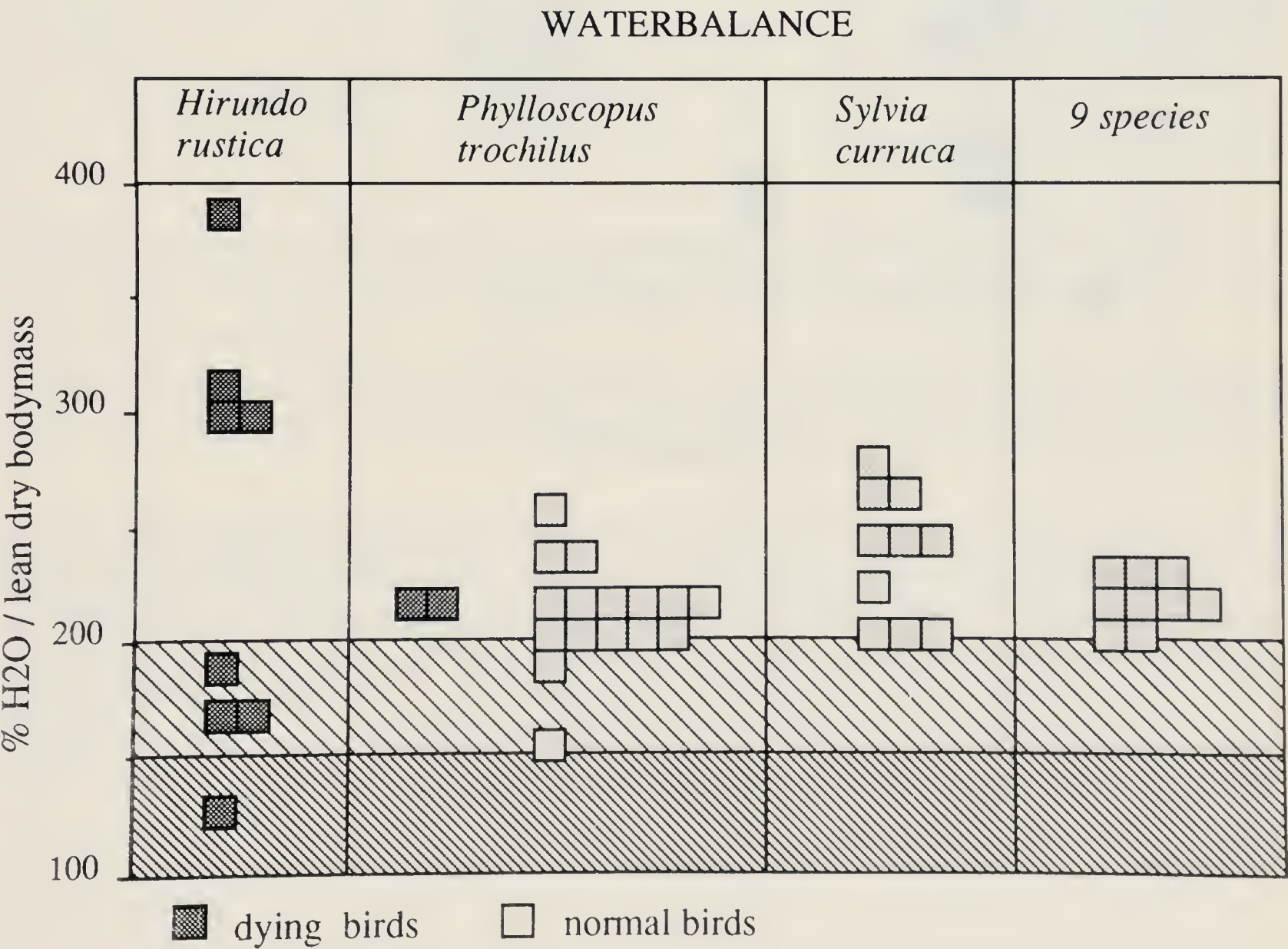


FIGURE 1 – Water content (% H₂O of lean dry bodymass) of migrants from three species, *Hirundo rustica*, *Phylloscopus trochilus* and *Sylvia curruca* sampled in autumn in the Libyan desert in Egypt and from nine species (means) killed at a television tower in Florida, North America on autumn migration. Dark squares are values from dying birds, light squares from birds with normal behavior. Birds with values above 200 are normally hydrated. Wide dashed zone is tolerance to dehydration, narrow dashed zone is lethal.

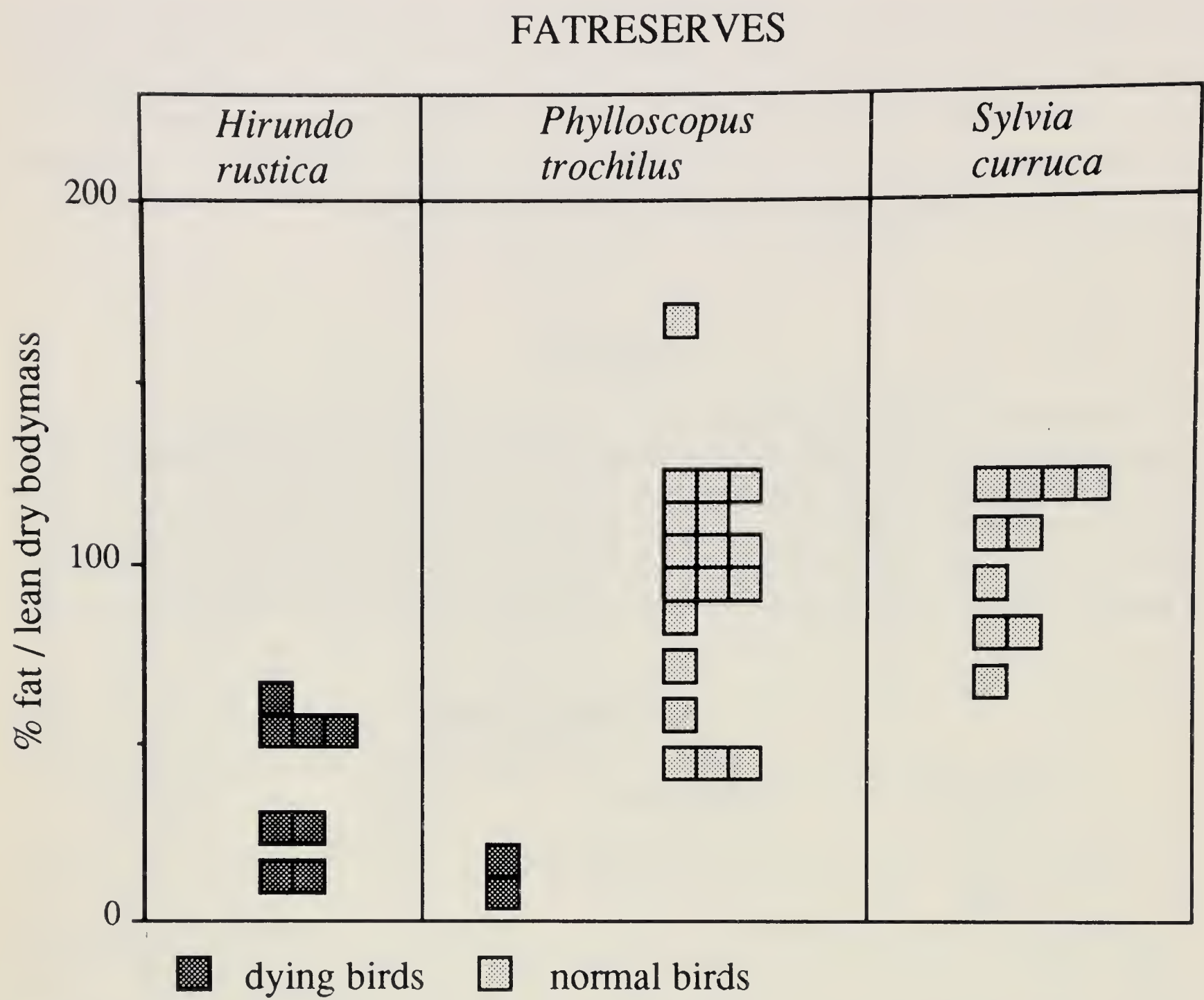


FIGURE 2 – Fat reserves (% fat of lean dry bodymass) of migrants from three species sampled in the Libyan desert in Egypt. Dark squares are values from dying birds, light squares represent birds with normal behavior.

far below 200 - the normal value of hydrated birds. This finding indicates that among normally resting birds, a few might be dehydrated. Two Willow Warblers that were classified as close to death were normally hydrated with values of 211 and 215. It is concluded that dehydration was not the reason for their condition. The water indices of the dying Swallows seem to fall into two groups: one group found in 1983 were all below an index of 200 and therefore more or less dehydrated whereas the Swallows found in 1982 had very high water indices well above 200 (Figure 1).

With respect to the fat reserves, the normal Willow Warblers and Lesser Whitethroats had moderate to extensive fat reserves with mean fat indices of 94 ± 32 (SD) ($n=18$) and 102 ± 20 (SD) ($n=10$) respectively. The two dying Willow Warblers had no fat left for metabolism. The group of Swallows with the high water indices still had moderate fat reserves with indices between 50 and 61 (Figure 2). The dehydrated group had no fat left for metabolism.

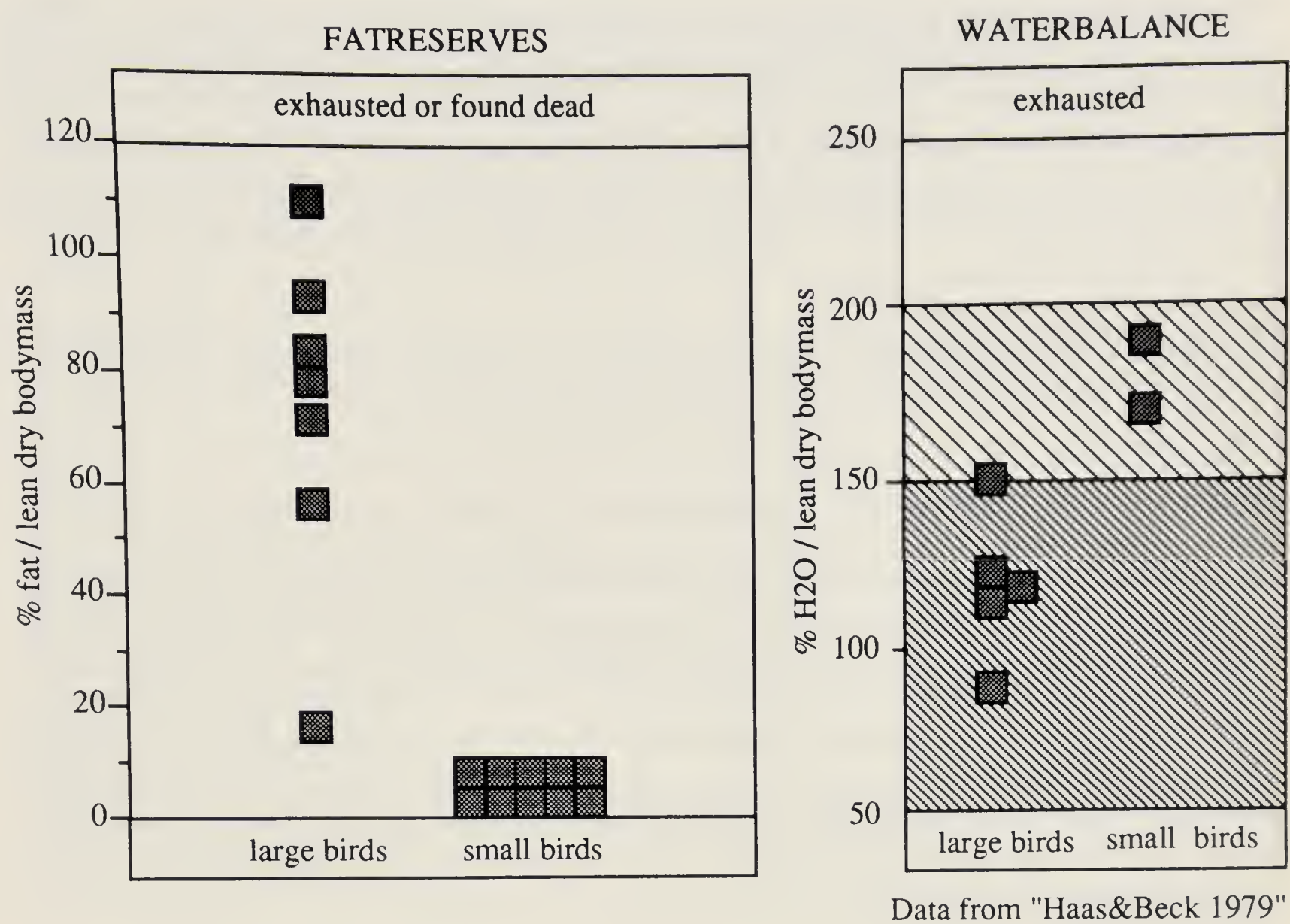


FIGURE 3 – Fat and water content of large (>50 g) and small (<50 g) migrants found dead or exhausted on spring migration in the Western Sahara. See also legend Figure 1. Data from Haas and Beck 1979.

DISCUSSION

Is fat as an energy source or is homeostasis of body water critical during long distance flights over the Sahara? The poor conditions of the Swallows cannot be explained simply by either of the two alternatives. They either had low fat and dehydration values or fat and dehydration values had not yet reached critical levels, though the birds were close to death. For this group of birds the physiological causes of their condition remain unclear. Swallows might be different from other small passerines, as they normally migrate during the daytime and are much more airborne than most other migrants. So, the role of dehydration as a limiting factor for Swallows remains to be elucidated. More data are necessary, especially from birds towards the end of the desert crossing.

The Willow Warblers and a sample of small passerines (bodymass<50 g) during spring migration in the Algerian Sahara (Haas & Beck 1979) showed no severe dehydration (Figure 3). On the other hand birds stopping-over for one day in the desert may lose as much as 20% of their total bodywater by evaporation and it is likely that

a second day of stopover brings them to critical levels of dehydration (Biebach 1990). Critical values of dehydration (below a water index of 150) have been reached by six exhausted, large birds (bodymass > 50 g) on spring migration (Haas & Beck 1979) (Figure 3). Their fat reserves were all robust. The conclusion is that water as a single limiting factor during desert crossing is still a matter of question. Possibly large birds are more susceptible to dehydration than small ones, as suggested already by Haas & Beck (1979).

Depleted fat reserves seemed to be the cause of energetic failure in the Willow Warblers (this study) and in small migrants analysed by Haas & Beck (1979) (Figure 3).

In addition to the fat extraction data reported here there is more information available concerning the fat reserves from three extensive samples of migrants from two sites in the Libyan desert in Egypt (Biebach et al. 1986) and from the Western Sahara (Bairlein 1985). Fat reserves were scored by inspecting the extent of subcutaneous fat depots in live birds (Cherry 1982). A fat score of 1, indicating no visible subcutaneous fat depots, corresponds quite well with low extractable fat. All six birds in the Swallow and Willow Warbler sample with extractable fat / lean dry mass below 30% had a fat score of 1. This value is taken as an indicator of birds that fail to cross the Sahara due to low fat reserves. Four percent of Lesser Whitethroats, 10 % of Willow Warblers, and 8 % of Yellow Wagtails *Motacilla flava* resting in an oasis in the Libyan desert had this low fat score. However, not one of the Lesser Whitethroats or Willow Warblers from a stopover site in a stony plain in the Libyan desert had a fat score of 1 (Biebach et al. 1986). In a sample of different passerine species resting in the Western Sahara about 24% of the birds had fat scores of 0 (which corresponds to 1 in the samples from Egypt because of different scaling – Bairlein 1985). One might conclude that a considerable number of migrants run out of lipid fuel during the desert crossing. However, we do not know to what extent the samples represent the majority of migrants. There are indications that birds resting in oases represent individuals with reduced energy reserves (Biebach et al. 1986). Therefore, we are unable to say how regularly the phenomenon of running out of fuel occurs.

As indicated earlier the current hypothesis of desert crossing suggests that an intermittent flight strategy is adopted because of unfavorable flight conditions. This strategy may occur when no air layer can be found that simultaneously satisfies tail wind and low air temperature requirements, and the birds are forced to stop flying. If the birds have to continue flying because no suitable stopover sites can be found we might tentatively conclude that the birds avoid high temperatures and go for headwinds. Under this scenario, they will then finally run out of fuel. These conclusions certainly need further confirmation and more data addressing the condition of birds at the end of the desert crossing are needed.

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PATTERNS OF AVIAN MIGRATION IN LIGHT OF CURRENT GLOBAL 'GREENHOUSE' EFFECTS: A CENTRAL EUROPEAN PERSPECTIVE

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ABSTRACT. There has already been a global increase in the mean temperature of about 0.6 °C since 1900, which has caused considerable concern among climatologists that there may be a further rise of between 1.5 and 5 °C over the coming decades. The increase is primarily due to a build-up of carbon dioxide in the atmosphere. A strong anthropogenic 'greenhouse' effect of this magnitude could alter the earth's vegetation and raise sea levels considerably. In addition, it would change bird life in general and migratory systems in particular. More specifically, residents would benefit from a decrease in winter mortality and an increase in reproductive output. Selective breeding experiments suggest that partial migrant populations would rapidly shift to sedentariness, and that short-distance migrants would shorten their migratory distances. Faced, then, with an overall increase in resident competition for resources, long-distance migrants would decline further. Some more detailed prognoses are given. Possible side effects of man-made climatic changes and other factors may cause an even more pronounced, general decline of avian diversity.

Keywords: 'Greenhouse' effects, central European bird fauna, migration systems, evolution, population dynamics.

INTRODUCTION

The present central European bird fauna has developed during the last postglacial period over the past 15000 years. The highest average species diversity and abundances were probably reached during the 18th century when the human settlement of large areas, and the alteration of closed woodland into highly structured mosaic landscapes, triggered the additional immigration of many open-country species. The decrease during the first half of the 19th century began slowly at first, but later accelerated. The population decline was initially caused by direct human persecution and later by anthropogenic impairment of all available ecosystems (for review, see Berthold 1990a). The present period is characterized by distinct global climatic changes most likely due to man-made alterations of the atmospheric gas composition (next section), and their accompanying 'greenhouse' effects, particularly a global warming tendency which has been predicted for the coming decades. Such basic environmental changes would certainly influence bird life in general and migration systems in particular. Up to now, few specific predictions for the relationships between global climatic changes and future bird life have been made (Berthold 1990a, Elkins 1990). Therefore some general predicted trends will be outlined here for central Europe.

MEASURABLE AND PREDICTED ANTHROPOGENIC 'GREENHOUSE' EFFECTS

Naturally occurring carbon dioxide and water vapor in the atmosphere absorb some of the long-wave radiation from the earth (mainly originating from the sun) which results in a natural 'greenhouse' effect where gas instead of glass acts as the absorber. Man-

made increases in CO₂, mainly due to the burning of fossil fuels and forest destruction, has led (in combination with other gases) to an enhancement of this effect, which has been termed the 'greenhouse' effect. The atmospheric CO₂ concentration has risen by 25% since pre-industrial times, with a rise of 11% alone in the past three decades. A further doubling of the concentration is expected by the middle of the next century. There has also been a concomitant global warming of about 0.6°C since 1900, most likely representing such a 'greenhouse' effect. Predictions for a further global rise in temperature, along with doubling of atmospheric CO₂, range between 1.5°C and 5°C (Figure 1), with the greatest increase in polar regions. The climatic patterns of 1989 follow this trend. In central Europe, it was the warmest year of this century with an elevation of 1.7°C above the mean temperature of the past 210 years.

If the predictions are substantiated, the melting of polar ice caps and mountain glaciers would raise sea levels considerably and would lead to an expansion of the oceans. Under this scenario, current sea-shore and estuarine habitats might well disappear to a large extent. Predictions with respect to precipitation are rather uncertain, but for higher latitudes an increase would be likely. This fits with the prediction of increased plant productivity. With a doubling of CO₂ concentration, the promoting effect could range between 25 % and 50 %. Increased primary production may, however, be accompanied by changes in nutrient dynamics, e.g. by a substantial decrease in the nitrogen content of plant material. Rather dramatic changes would then be expected in the distribution of vegetation belts. More southern plant communities could rapidly spread north, and coniferous forest could be replaced by deciduous woodland over large areas. There would, however, be a risk of considerable plant mortality with subsequent loss of the accompanying microfauna and thus dramatic changes in the present ecosystems. The arctic tundra may completely disappear as a habitat due to the extension of shrubby plants from the south and to inundation from northern seas. Further predictions concern a general increase in extreme climatic events like more irregular occurrence of wet and dry periods, increased probability of heatwaves, and storms. These events may exert negative effects on sensitive parts of ecosystems, and storms may increasingly destroy forests. For more details see, e.g., Anonymous (1990), Dobson et al. (1989), Boer et al. (1990), Elkins (1990), Roczniak (1990).

GENERAL ASPECTS OF EXPECTED CHANGES IN BIRDLIFE

A general warming, especially during autumn, spring and winter, and an increase in primary production should primarily favour resident species. Reduced winter mortality and earlier breeding seasons could theoretically lead to major increases, especially in species with r-strategies such as tits, which normally compensate for high winter mortality with high reproductive rates. There are already indications for current population increases in eastern European tit populations (Berthold 1990a). In western populations, however, possible increases may have been suppressed by negative man-made environmental effects like deforestation due to storm damage, the 'Waldsterben', and more direct effects of acid rain. In Holland, Great Tit *Parus major* breeding data in areas of nutrient-poor soil, has demonstrated an increase of more than 50 % in the percentage of territorial pairs with no eggs or disturbed eggshell formation since 1983. The inferior quality of eggshells is assumed to be the result of an insufficient calcium content in food and plant material due to acid rain. Meanwhile, there are similar reports for central Germany (for review, see Berthold 1990a). Thus, a general mass increase in residents may well be prevented in a number of species by counteracting negative environmental factors.

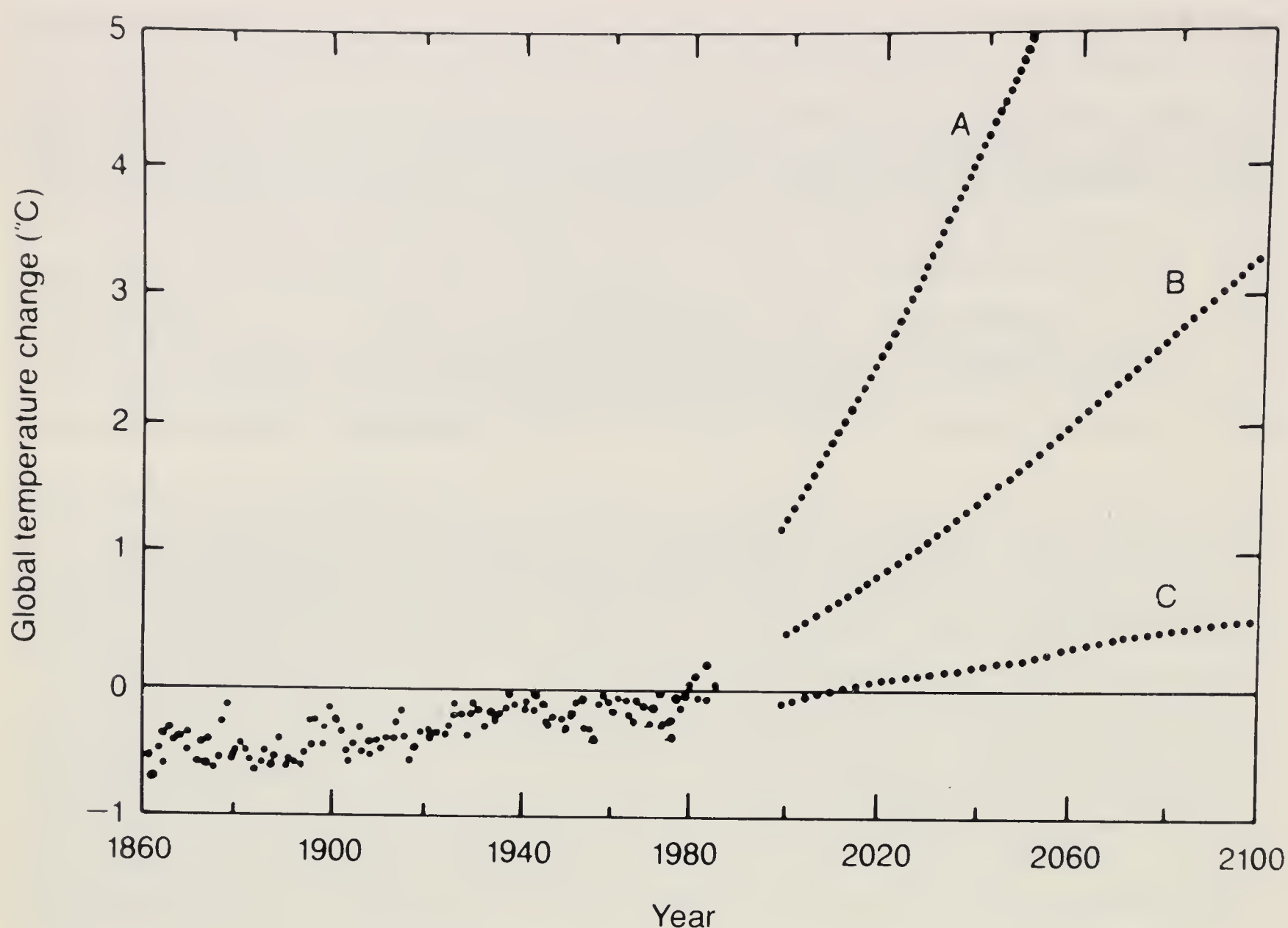


FIGURE 1 – Global temperature change in °C 1860-1984 and predicted temperature changes according to three models (A-C, from Dobson et al. 1989).

Other groups which should be generally favoured by predicted environmental changes are partial and middle to short distance migrants which winter south to the Mediterranean. Selective breeding experiments with partially migratory Blackcaps *Sylvia atricapilla* have recently shown that under strong selection pressure, genetically based sedentariness can be expected within four to six generations (Figure 2). Current selective breeding experiments with Blackcaps indicate that there is also a fairly high heritability with respect to the amount of migratory activity within populations which controls the distance of migration. Warmer autumn, winter and spring periods should thus (1) rapidly shift the proportions of obligate partially migratory species towards sedentariness, and (2) individuals of middle to short distance migrants should continuously be selected for shorter migration distances. After the mild winters of the past few years, local ornithological reports from central European areas have recorded numerous observations of partial and short-distance migrants wintering within the breeding area.

The obvious losers in light of the predicted environmental changes should, in general, be long-distance migrants. These species have already shown more marked population declines than any other group of European birds. These decreases are, however, due to many factors. A major problem is, undoubtedly, the Sahel drought (e.g. Berthold 1990b). Multifactorial analyses of the British Trust for Ornithology (O'Connor 1981) and direct studies of competitive behaviour (for review, see Berthold 1990a)

have clearly demonstrated that the successful settlement of late arriving, long-distance migrants on the breeding grounds depends on the density of resident species and short and middle distance migrants which have already established territories. Substantial increases in both residents and short to middle distance migrants should therefore lead to decreases in long-distance migrant populations. These declines may even result in extinction of those groups for which large-scale habitat loss is likely (e.g., in coastal and tundra areas). Thus, the predicted environmental changes will most likely substantially reduce long-distance migration and promote sedentariness and short-distance migration. The only alternative for long-distance migrants, the shift to short-distance migratory behaviour by microevolutionary processes, is probably too slow an alteration to occur in time.

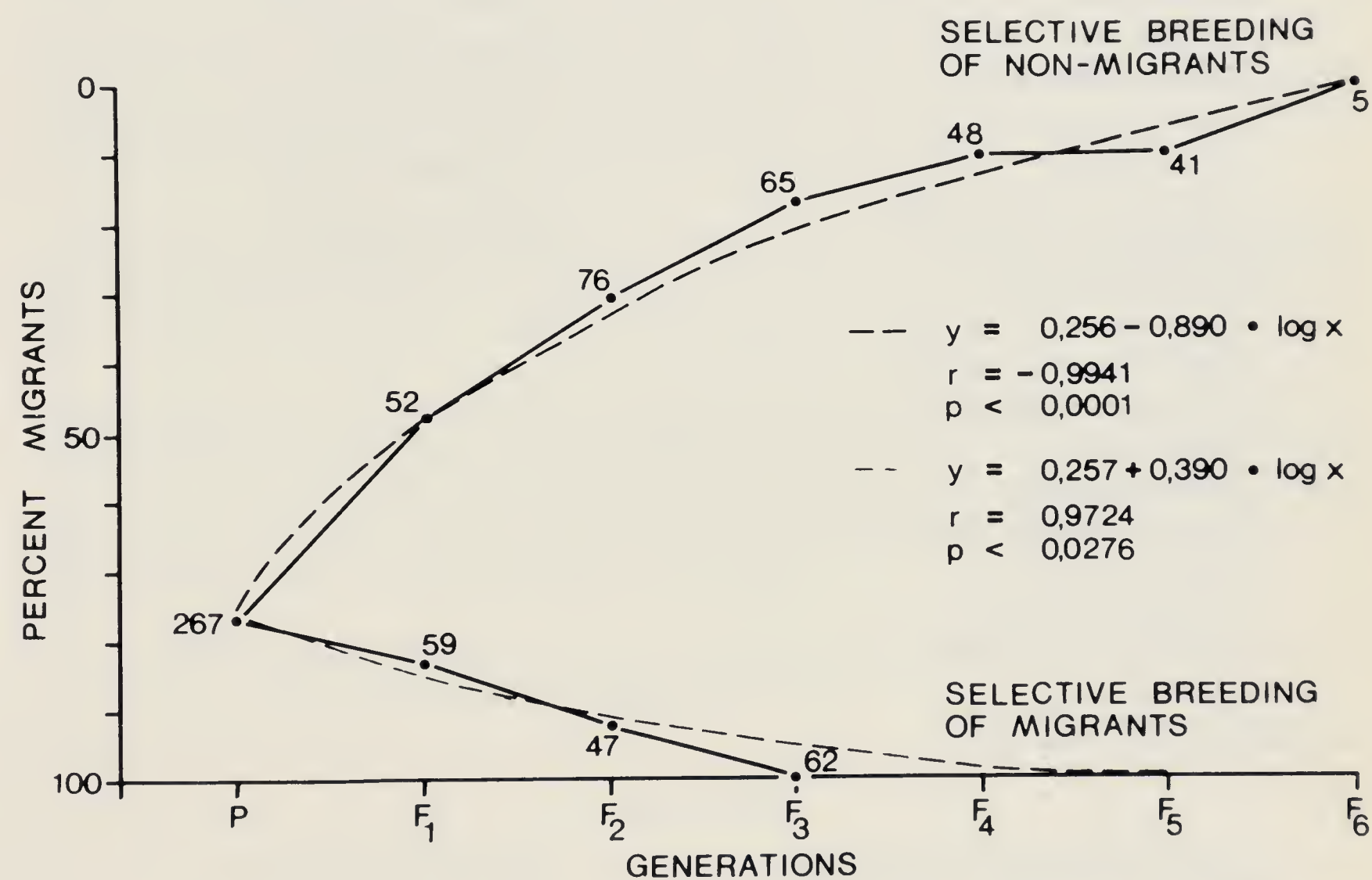


FIGURE 2 – Results of a two-way selective breeding experiment with partially migratory Blackcaps from southern France up to the F6-generation (nonmigrants) and to the F3-generation (migrants). Numbers: individuals bred in each generation, broken lines: mathematical functions that best fit to the selection response (from Berthold et al. 1990).

SOME SPECULATIONS ABOUT INDIVIDUAL SPECIES

In general, in all three groups of birds, i.e. residents, short to middle distance migrants and long-distance migrants, generalists will have a far better chance of coping with the predicted environmental changes than specialists. For example, among residents, specialists for coniferous forests such as the Coal Tit *Parus ater* are already declining and will presumably be further affected whereas generalists such as the Greenfinch *Chloris chloris* or Tawny Owl *Strix aluco* will most likely increase. Further, with respect to deforestation, species which inhabit shrubbery will be more successful than forest specialists.

TABLE 1 – Four categories of central European bird species with predicted different population trends.

Partial and short- to middle-distance migrants

A	B
with high chances for population increase	with lower chances for population increase
<i>Phalacrocorax carbo</i>	<i>Grus grus</i>
<i>Ardea cinerea</i>	<i>Vanellus vanellus</i>
<i>Buteo buteo</i>	<i>Columba palumbus</i>
<i>Fulica atra</i>	<i>Alauda arvensis</i>
<i>Larus ridibundus</i>	<i>Anthus pratensis</i>
<i>Alcedo atthis</i>	<i>Turdus viscivorus</i>
<i>Motacilla alba</i>	<i>Turdus philomelos</i>
<i>Troglodytes troglodytes</i>	<i>Emberiza citrinella</i>
<i>Prunella modularis</i>	<i>Sturnus vulgaris</i>
<i>Sylvia atricapilla</i>	
<i>Phylloscopus collybita</i>	
<i>Phoenicurus ochruros</i>	
<i>Erithacus rubecula</i>	
<i>Turdus pilaris</i>	
<i>Turdus merula</i>	
<i>Emberiza schoeniclus</i>	
<i>Serinus serinus</i>	
<i>Carduelis carduelis</i>	
<i>Carduelis cannabina</i>	

Long-distance migrants

C	D
being endangered to decline strongly or to die out over the next decades	with good chances for long-term survival
<i>Ixobrychus minutus</i>	<i>Milvus migrans</i>
<i>Ciconia ciconia</i>	<i>Hirundo rustica</i>
<i>Anas querquedula</i>	<i>Delichon urbica</i>
<i>Jynx torquilla</i>	<i>Apus apus</i>
<i>Lanius senator</i>	
<i>Acrocephalus palustris</i>	
<i>Acrocephalus schoenobaenus</i>	
<i>Sylvia curruca</i>	
<i>Sylvia communis</i>	
<i>Saxicola rubetra</i>	
<i>Phoenicurus phoenicurus</i>	

In Table 1, four categories of species are listed with respect to population trends. Category A summarizes central European partial and short to middle distance migrants which presently show either increasing or stable populations (e.g. Berthold et al. 1986). Under the predicted environmental changes, these species could readily shift to more-or-less complete sedentariness which would strongly enhance their populations. Most of these species are, in many respects, generalists and should also be able to cope with changing ecosystems. The few specialists such as *Phalacrocorax* and *Alcedo* would benefit from human activities.

Category B summarizes potentially favoured species where additional circumstances are more limiting. In *Grus grus* and *Columba palumbus*, for instance, the destruction of Mediterranean oak woodland as the basis for successful wintering may exert increasing negative effects (e.g. Gatter et al. 1990). In the other species, habitat loss has either already led to strong population declines like *Vanellus vanellus* and *Anthus pratensis* which are already on the German list of endangered species, or may, in combination with other factors, hinder potential population increase.

Endangered long-distance migrants are listed under category C. These are species that have already declined substantially and, under the scenario of habitat changes and increased competition, might even disappear.

In Category D, finally, four migratory species with presumably good chances for long-term survival are listed. All of them are able to feed continuously during migration and thus may overcome impaired conditions during migration in the future. Among these species, the Swallow and the Swift would have practically no competitors, even in a considerably altered central European bird fauna.

For all other central European bird species not listed in the table, predictions are, in my opinion, much more difficult to make at this time.

OUTLOOK

I have to emphasize that the hypothesized changes in central European birdlife during the coming decades due to anthropogenic 'greenhouse' effects can only be made with a high degree of uncertainty. Additional changes in ecosystems not considered here may strongly affect various species. For example, the current dramatic increase in the amount of forest fires in the Mediterranean region may destroy wintering grounds for many short and middle distance migrants before these species are able to develop into more sedentary populations. If desertification of the borderland of the Sahara desert reaches the Mediterranean areas, as some climatologists predict, it is uncertain how many long-distance migrants would continue to be capable of crossing such an expansive, dry area to winter south of it in Africa. Additionally, wintering by short-distance migrants in the Mediterranean might well become improbable. Taking into account all the possibilities, a continued overall reduction of species diversity of central European birdlife is likely. Further anthropogenic climatic changes appear currently highly likely with long-distance migrants suffering most from major negative effects of these changes.

ACKNOWLEDGEMENT

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CLOSING REMARKS: NEW ASPECTS OF AVIAN MIGRATION SYSTEMS

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Just over a decade ago, S. A. Gauthreaux (1979) lamented justifiably the lack of breadth in our study of bird migration and expressed particular concern that proper emphasis was not being placed on the ecology and evolution of migration. The papers presented in this symposium as well as other invited and contributed papers to the XX International Ornithological Congress suggest that “doldrums” is no longer an apt metaphor for research on bird migration. Besides recognizing the progress made in the study of bird migration, I wish to emphasize two, not unrelated, issues raised during this symposium.

Not long ago, M. Pienkowski and P. Evans (1985) observed that “...the remarkable lengths of regular migratory journeys by many birds are now so well established that some biologist seem to discount their costs.” Contributions to this symposium focused attention on the factors that contribute to the costs of migration and on the adaptations that have evolved to offset these costs. While en route, a passage migrant must forage in unfamiliar habitats to replenish depleted energy stores, resolve conflicting demands of predator avoidance and food acquisition, compete with other migrants and resident birds for limiting resources, including food and water, respond to unpredictable and sometimes unfavorable weather, and correct for orientation errors. Moreover, favorable habitat, where a migrant can safely and rapidly meet physiological demands, is probably limited, or effectively so because it may not always have the opportunity to select the best habitat.

Second, conservation efforts on behalf of intercontinental bird migrants depends on knowing when, where, and how migrant populations are regulated. Answers to those questions require a comprehensive interdisciplinary program of research — one that recognizes the relationship between behavior and population biology. Achievement of this disciplinary “synthesis” may not be easy. Behavioral ecologists are usually concerned with the way the behavior of animals may have evolved, with little reference to the consequences such behavior may have for population dynamics. Conversely, population biologists usually focus on the demographic consequences of environmental or biological changes, with little reference to behavioral mechanisms that may underlie changes in birth, death and migration rates. They deal with fundamental demographic processes of births, deaths, immigration and emigration and factors affecting them, and the challenge is to expose the crucial factors underlying the patterns or distribution and abundance of a population over a time-scale of several generations. Although there is an enormous literature on migration and dispersal, there are very few studies explicitly relating these phenomena to the magnitude and stability of the populations in question. One obvious exception is the work on temperate-tropical bird migrants which seeks to comprehend the population dynamics of particular

species in terms of measurable parameters characterizing the migratory and reproductive behavior of individuals. Palearctic-African and Nearctic-Neotropical bird migration systems represent prime examples of a situation where a phenomenological description of the way populations interact in a spatially heterogeneous environment can, on the one hand, be grounded on an understanding of the behavior of individuals and, on the other hand, lead to insights about population dynamics and community structure. The relevance to the conservation of our intercontinental migrants is obvious.

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SYMPOSIUM 11

**ECOLOGICAL AND EVOLUTIONARY
CONSEQUENCES OF BODY SIZE**

Conveners B. A. MAURER and J. F. PIATT

SYMPOSIUM 11

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INTRODUCTORY REMARKS: ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF BODY SIZE

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Most ornithologists inevitably give some consideration to the consequences and implications of body size. Variation in body size within and among species has provided a general framework for interpreting ecological adaptations (e.g., Bergmann's rule), evolution (e.g., Cope's law), competition and species diversity. During the last few decades, the study of allometry has yielded a quantitative basis for interpreting relationships between body size and other biological parameters. The strength and ubiquity of allometric trends have allowed us to go beyond the explanation of patterns we observe to the prediction of characteristics we cannot otherwise measure.

The study of allometry can be broken down into five main components: structure, growth, physiology, behaviour and ecology. The allometry of structure, growth and physiology has been well studied. The scaling of individual body parts in relation to the overall size of birds is often constrained by structural principles. Body parts grow at predictable rates for a given body size, and different species grow at rates that are scaled to their size. The physiological parameters of metabolic rate and turnover of materials are scaled to body size. In each of these three disciplines, it has been found that body size often accounts for 90-99% of the variation in measured parameters — presumably because structure, growth, and metabolism are governed largely by the laws of physics and chemistry. In many cases this scaling is linear. For example, large birds need proportionately as much intestine as small birds to process food. In many instances, however, this scaling is non-linear because of the "economies of scale". The most familiar example of this is the scaling of metabolic rates to $M^{0.75}$ (Kleiber's 3/4 Rule). Because small birds lose more heat on a gram-per-gram basis than large birds, they must maintain a higher metabolic rate than large birds.

The last two components of allometry — behaviour and ecology — have been studied less and are the focus of this symposium. We observe that certain behaviours, for example foraging time and distance, sleep, prey selection, sociality, social dominance, etc., are scaled with body size in many taxa. In allometric ecology, we consider the constraints that body size imposes on mass and energy flow, reproduction, and population dynamics. Through consideration of allometric constraints, we hope to gain insight on evolution and natural selection. Such studies are especially challenging because many of the behavioural and ecological parameters that we can measure are often poorly correlated with body size for a variety of reasons. For example, behaviour is quite variable within and between species and often difficult to measure in a standardized fashion. Lumping of different groups may obscure trends that exist within taxa or coexisting guilds. Nonetheless, allometry offers a quantitative and well-established starting point from which we can proceed to understand avian ecology. Once

we account for ecological variability owing to body size, we can perhaps assess the degree to which other factors determine patterns of bird abundance and distribution. This understanding may be useful in a world with rapidly changing environments.

In the following series of papers, we consider some of the ecological and evolutionary consequences of body size in birds. Kenneth Nagy and Bryan Obst begin by examining how field metabolic rates of birds vary with body size and consider what may account for the residual variation in metabolism after the effects of size are removed. William Calder and Cynthia Carey discuss the use of allometry in scaling avian ecology and consider how allometry may be applied to practical management and conservation issues. Ian Goudie and John Piatt examine the relationship between body size and foraging time budgets in birds and consider how body size constrains behavioural flexibility in variable or extreme environments. Terry Root examines the role of body size in limiting species distribution by considering the implications of body size for competition, adaptation to extreme environments, habitat use, and prey selection. Finally, Brian Maurer, Eduardo Rapoport and Hugh Ford compare the distribution and diversity of Australian and North American avifauna, and consider the role of body size in maintaining diversity and influencing time to extinction for various taxa.

BODY SIZE EFFECTS ON FIELD ENERGY REQUIREMENTS OF BIRDS: WHAT DETERMINES THEIR FIELD METABOLIC RATES?

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ABSTRACT. Field metabolic rates (FMRs) of birds, measured with doubly labeled water, range from 27 kJ/day (0.31 W) in hummingbirds to over 4730 kJ/day (54.8 W) in Giant Petrels, a range of 175-fold. Most of this variation is due to differences in body mass. However, after recalculating FMR values in units of $\text{kJ g}^{0.64} \text{d}^{-1}$ to account for mass differences, a 6-fold variation in FMR still remains. What accounts for this residual variation? High FMRs occur in passeriform and charadriiform birds, carnivorous birds, seabirds (carnivorous birds that forage widely) and birds that live in meadows or marshes. However, these phylogenetic and ecological categories alone do not satisfactorily explain the large residual variation in FMR, partly because of small sample sizes available to date, but also because variation due to season, gender, daily behavior pattern, ambient temperature, social organization, flight mode and duration, food availability and predator pressure is real but is not accounted for in the above categories.

INTRODUCTION

The fitness of a bird may be determined in large measure by how successfully it obtains the food it needs for its own growth and maintenance and for production of viable offspring. Feeding rate is very difficult to measure directly in the field. However, because a large fraction of food energy is metabolized to heat by birds, measurements of field metabolic rate (FMR), which are readily obtained via the doubly labeled water (DLW) method, can serve as the basis for estimates of food requirements of free-living birds (Nagy 1989). Thus, DLW measurements of FMR can be valuable in evaluating the impact of an environment on the birds living there, as well as the impact of the birds on their environment, in terms of food resources consumed by the birds.

It is unlikely that the field energetics of all bird species under all circumstances will be directly measured by biologists. Thus, it is important to derive ways to predict the food and energy requirements of birds, and to evaluate the accuracy and reliability of such predictions. Many factors are known to influence the energy and food requirements of free-living birds, but body mass is thought to have the largest effect. In this paper, we examine the importance of body size (mass) in explaining the variation in observed FMRs of birds, and then we use analysis of residuals, after correction for body size effects, to try to account for the variation that still remains.

MATERIALS AND METHODS

The data set we used consisted of all the published studies of FMR in birds, as measured with the doubly labeled water method, known to us at the time this analysis was done (21 January 1989). We included data for 25 species from an earlier review (Nagy

1987) along with new data for an additional 15 species (Table 1). We restricted our analysis to properties of entire species, such as mean body mass, diet and habitat, and did not consider within-species variables (such as gender) in this analysis. When separate FMR and body mass values were reported for different seasons, age groups, study plots, etc. within a species, we used the mean of these values to represent the species as a whole.

TABLE 1 - Summary of doubly labeled water measurements of birds published since the review by Nagy (1987).

Species	Body mass, g	FMR, kJ/day	Reference
Coal Tit <i>Parus ater</i>	9.5	47.4	Moreno et al. 1988
Crested Tit <i>Parus cristatus</i>	11.1	40.6	Moreno et al. 1988
Willow Tit <i>Parus montanus</i>	11.3	41.2	Moreno et al. 1988
Tree Swallow <i>Tachycineata bicolor</i>	22.4	118	Williams 1988
Leach's Storm-petrel <i>Oceanodroma leucorhoa</i>	44.8	87.1	Ricklefs et al. 1986
Dipper <i>Cinclus cinclus</i>	63.1	220	Bryant & Tatner 1988 Bryant et al. 1985
Pied Kingfisher <i>Ceryle rudis</i>	76	210	Reyer & Westerterp 1985
Least Auklet <i>Aethia pusilla</i>	83.5	358	Roby & Ricklefs 1986
South Georgia Diving Petrel <i>Pelecanoides georgicus</i>	109	464	Roby & Ricklefs 1986
Common Diving Petrel <i>Pelecanoides urinatrix</i>	137	557	Roby & Ricklefs 1986
Eurasian Kestrel <i>Falco tinnunculus</i>	220	343	Masman et al. 1988
Black Guillemot <i>Cepphus grylle</i>	420	640	Roby & Ricklefs 1986
Thick-billed Murre <i>Uria lomvia</i>	834	1475	Roby & Ricklefs 1986
Little Penguin <i>Eudyptula minor</i>	1089	997	Costa et al. 1986
Grey-headed Albatross <i>Diomedea chrysostoma</i>	3706	2401	Costa & Prince 1987

We used linear least-squares regression analysis for characterizing allometric relationships for FMR. Confidence intervals (95% CI) were used to evaluate (1) differences between predicted and measured FMRs, (2) differences between allometric relationships, and (3) differences due to taxonomic, dietary and habitat characteristics of groups of species. The latter characteristics cannot be expressed as numerical values, making multiple regression procedures inappropriate for our purposes.

BODY SIZE (MASS)

FMRs of birds studied to date range from about 27 kJ/day for hummingbirds to over 4730 kJ/day for Giant Petrels (Nagy 1987; Table 1), a range of 175-fold. Differences in body mass (as log Mb) account for about 91% of the variation in log FMR ($r^2 = 0.907$ for the \log_{10} - \log_{10} regression of FMR upon body mass for the 50 data points on 25 species available in 1987). The present availability of data points for 15 additional species affords us an opportunity to address three questions. First, how well does the equation: $\text{kJ/day} = 10.9 \text{ g}^{0.64}$, based on the 1987 data, predict the FMRs of the recently-studied species? Second, does addition of the new results to the allometric relationship for birds yield a different equation than that for 25 species? Third, does the addition of 15 more data points “explain” more variation (i.e. does r^2 increase)?

TABLE 2 - Relative field metabolic rates (FMRs, adjusted for body mass effects) of 40 species of birds (from Nagy 1987 and Table 1). Common names from Clements (1978).

Common name	Log ₁₀ mass	FMR, % pred. ^a	ord. ^b	diet ^c	hab.
Anna's Hummingbird	0.65	94	AP	N	CS
Grey-breasted Silvereye	0.98	91	PA	F	EF
Coal Tit	0.98	103	PA	I*	CF
Crested Tit	1.05	80	PA	I*	CF
Willow Tit	1.05	80	PA	I*	CF
Pacific Swallow	1.15	129	PA	I*	TF
Sand Martin	1.16	137	PA	I*	TM
Savannah Sparrow	1.27	112	PA	O	SM
House Martin	1.28	111	PA	I*	TM
Swallow	1.31	138	PA	I*	TM
Tree Swallow	1.35	148	PA	I*	TM
Phainopepla	1.36	98	PA	O	D
Blue-throated Bee-eater	1.53	72	CO	I**	TF
Wilson's Storm-petrel	1.63	99	PR	C*	M
Leach's Storm-petrel	1.65	71	PR	C*	M
Mockingbird	1.68	94	PA	O	DF
Purple Martin	1.69	124	PA	I*	DF
Dipper	1.80	143	PA	I*	TM
Pied Kingfisher	1.88	118	CO	C*	TF
Starling	1.90	151	PA	O	DF
Least Auklet	1.92	207	CH	C*	M
South Georgia Diving Petrel	2.04	211	PR	C*	M
Common Diving Petrel	2.14	220	PR	C*	M
Gambel's Quail	2.16	34	GA	O	D
Sooty Tern	2.27	78	CH	C*	M
Sand Partridge	2.28	47	GA	O	D
Brown Noddy	2.29	111	CH	C*	M
Eurasian Kestrel	2.34	100	FA	C**	TM
Wedge-tailed Shearwater	2.58	125	PR	C*	M
Black-legged Kittiwake	2.59	185	CH	C*	M
Chukar	2.60	52	GA	O	D
Black Guillemot	2.62	123	CH	C*	M
Thick-billed Murre	2.92	183	CH	C*	M
Little Penguin	3.04	104	SP	C*	M
Laysan Albatross	3.49	97	PR	C*	M
Jackass Penguin	3.50	103	SP	C*	M
Grey-headed Albatross	3.57	115	PR	C*	M
Adelie Penguin	3.59	186	SP	C*	M
Giant Petrel	3.61	200	PR	C*	M
Wandering Albatross	3.92	93	PR	C*	M

^a Field metabolic rate, as percent of that predicted from body mass (in g) from the equation: FMR (in kJ/day) = 10.9 g^{0.67} (Nagy 1987).

^b Order: AP = Apodiformes, PA = Passeriformes, CO = Coraciiformes, PR = Procellariiformes, CH = Charadriiformes, GA = Galliformes, FA = Falconiformes, SP = Sphenisciformes.

^c Diet: N = nectar, F = fruit, I = insect, O = omnivore, C = carnivore, * = wide-foraging predator, ** = sit-and-wait predator.

^d Habitat: CS = chaparral scrub, EF = eucalypt forest, CF = coniferous forest, TF = tropical forest, TM = temperate meadow, SM = salt marsh, D = desert, M = marine, DF = deciduous forest.

To test the predictive capability of the 1987 equation, we solved it using the mean body mass for each new species, and then calculated the 95% CI of the prediction (which is much larger than the 95% CI of the regression, due to the increased uncertainty expected for new data points; see Dunn and Clark 1974, and Figure 5 and Discussion in Nagy 1987 for more details). Comparison of predicted with measured FMR values revealed that all 15 new measurements fell within the 95% CIs of the predictions. The new measurements averaged 133% of predicted FMR values (range 71 to 220% of predicted). Thus, the predictive capability of the 1987 equation is good.

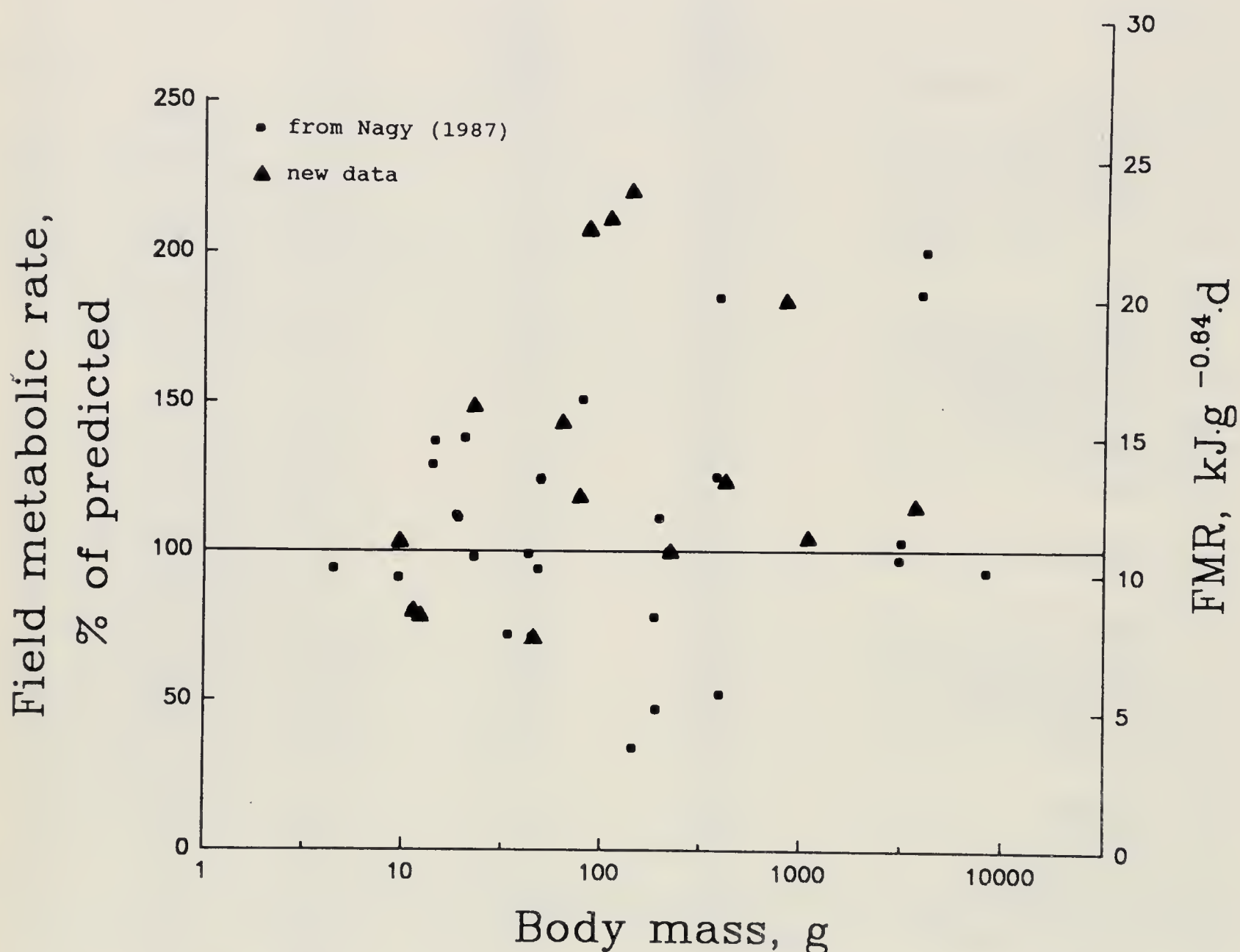


FIGURE 1 - Mass-independent field metabolic rates of 40 species of birds. Horizontal axis is a logarithmic scale. Closed circles represent data taken from Nagy (1987), and filled triangles represent new data published subsequently (Table 1).

Does the addition of new data change the allometric relationship for FMR in birds? The 1987 equation included multiple data points for some species, in order to incorporate as much variation in the regression as actually occurs in different cohorts or between seasons within species. To simplify comparison of old and new data, we recalculated the old regression using only species means for body mass and FMR ($n = 25$). The resulting equation, $\text{kJ/day} = 10.1 \text{ g}^{0.66}$, does not differ significantly from the 1987 equation, judging by the observations that the intercept (10.1, 95% CI = 6.5 to 15.5) falls within the 95% CI of the 1987 intercept (10.9, 95% CI = 8.1 to 14.7), and the slope (0.66, 95% CI = 0.58 to 0.74) falls within the 95% CI of the 1987 slope (0.64, 95% CI = 0.58 to 0.70). The addition of data points for 15 new species yields the equation $\text{kJ/day} = 10.4 \text{ g}^{0.67}$ ($N = 40$, 95% CI of intercept = 7.5 to 14.6, 95% CI of slope = 0.60 to 0.73). The intercept and slope of this equation fall within the 95% CIs

of both of the above equations. Thus, the new data support the descriptive capability of the 1987 equation.

Does addition of the new data improve the regression equation's "explanatory" property (higher r^2 value)? The r^2 values are 0.907 (1987 equation, 50 points for 25 species), 0.923 (1987 data, 25 points for 25 species), and 0.919 (40 points for 40 species). Assuming that an r^2 value reflects the amount of variation in y explained by variation in x , then all three regressions indicate that variation in log body mass accounts for 91 to 92% of the variation in log field metabolic rate among species of birds. The addition of data for 15 new species did not substantially increase r^2 , indicating that the 1987 equation accurately reflects variation in FMR among bird species.

RESIDUAL VARIATION

Much variation still remains in FMRs of birds after accounting for body mass influences. We recalculated FMR values by dividing by $g^{0.64}$ to "correct" for size effects. If differences in mass completely accounted for differences between species, all values for $\text{kJ } g^{-0.64} \text{ day}^{-1}$ would be 10.9. In fact, mass-independent FMRs range from 34 to 220% of this value (Figure 1). Thus, the 175-fold variation in whole-animal FMR is largely explained by differences in body mass, but a six-fold variation remains unexplained. We examined this residual variation for trends associated with taxonomic group (order), diet and habitat, in an attempt to improve our accuracy in predicting FMRs of birds.

We tested for a difference between the mean mass-independent FMR for a given group and the predicted value of $10.9 \text{ kJ } g^{-0.64} \text{ d}^{-1}$ by determining whether the 95% CI for a group included the predicted value, and by means of a t-test. Results are shown as percent of the predicted value.

Phylogeny

Passeriform birds ($n = 14$ spp.) had mass-corrected FMRs averaging 116% (95% CI = 102 - 130%) of the predicted value. This difference is just barely significant statistically ($P = 0.05$). Similarly, the 7 species of charadriiform birds studied also had significantly higher than expected FMRs, with a mean of 145% (95% CI = 101 - 189%). However, the FMRs of procellariiform birds (8 spp.) averaged 138% (95% CI = 87 - 189%) of predicted, which is not a statistically significant difference. With a very small sample size ($n = 3$), galliform FMRs averaged only 44% of predicted (95% CI = 21 - 67%), the lowest of any taxon.

Diet

Insectivorous birds (115% of predicted FMR, 95% CI = 96 - 134%, 11 species) and omnivorous birds (84%, 95% CI = 45 - 123%, $n = 7$) did not differ significantly from predicted, but carnivorous birds had higher FMRs (136% of predicted, 95% CI = 113 - 159%, $n = 20$). Among the insectivores and carnivores, those we judged to be widely-foraging species had high FMRs (132% of predicted, 95% CI = 115 - 149%, $n = 28$), whereas the three "sit-and-wait" (ambush predator) species had FMRs typical of other birds (97%, 95% CI = 39 - 155%).

Habitat

Forest-dwelling species did not have unusual FMRs (mean = 103% of predicted, 95% CI = 87 - 120%, $n = 11$), but meadow- and marsh-dwelling species had relatively high FMRs (127%, 95% CI = 112 - 144%, $n = 7$). Terrestrial nondesert birds (forest, meadow and marsh habitats taken together) had moderately high FMRs (113%, 95% CI = 101 - 125%, $n = 18$). Desert birds tended to have low FMRs (but not significantly lower than average: 58% of predicted, 95% CI = 14 to 102%, $n = 4$), whereas seabirds had high FMRs (140%, 95% CI = 115 - 165%, $n = 18$).

DISCUSSION

Body mass clearly has the largest influence on the field metabolic rate of birds. Once size effects are accounted for, however, much variation (6-fold) still remains. Although the above analyses suggest that phylogeny and ecology may have moderate (ca. 3-fold) effects on FMR, they do not satisfactorily account for the large residual variation in mass-corrected FMR. Several reasons are probably involved. First, current sample sizes within categories are perhaps too small to demonstrate important influences. Moreover, strong biases can emerge with small samples, e.g. four of seven species from meadow habitats are swallows. Second, these broad categories incorporate measurements that include variation due to season, gender or behavior. The few studies that address these factors within a single species indicate that interseasonal variations in FMR range from 1.2- to 1.5-fold, that FMRs at various phases of the breeding season may differ up to 2.5-fold, and that differences due to gender may be 1.3-fold. Third, categorizations of diet (e.g. "omnivore") and habitat (e.g. "the sea") are very broad and may be useful only insofar as they accurately describe the species' ecology at the time of measurement.

Finally, ecological and phylogenetic categories often overlap, such that the independent effects of each cannot easily be sorted out: nearly all carnivorous birds measured are seabirds; the passerines studied to date are nearly all insectivores or insect-eating omnivores. Other factors worth investigating include ambient temperature, social organization, flight mode and duration, food availability, and predator pressure.

At present, it appears that no single factor accounts for all, or even much, of the residual variation in FMR that is not accounted for by body mass. Several of these factors are probably involved in determining a bird's FMR. For example, the four species having the highest mass-corrected FMRs (the Least Auklet, the South Georgia Diving Petrel, the Common Diving Petrel, and the Southern Giant Petrel) are all carnivorous seabirds that live at high latitudes and spend much time flying and/or have high wing loadings. The three species with the lowest mass-corrected FMRs (Gambel's Quail, Sand Partridge, and Chukar Partridge) all live in warm deserts, fly infrequently, are in the order Galliformes, and are omnivorous (but primarily granivorous). It may eventually become possible to identify and quantify the major factors influencing FMR in enough detail to permit accurate prediction of FMR in birds (e.g. within 10-15%), but present information provides predictive equations (Nagy, 1987) that are only accurate to between -50% and +100% (95% CI of predicted kJ/day value).

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SCALING AVIAN ECOLOGY

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ABSTRACT. Interspecific scaling patterns derived from laboratory data have facilitated analysis of many physiological and morphological variables of both embryonic and adult birds. Some of these variables (e.g. metabolic rates, turnover times) have ecological parallels (e.g. home range, longevity). Correlations for scaling relationships calculated from organismic data collected in the laboratory are generally much higher than are ecological ones; ecological relationships are complicated by a number of uncontrollable variables like spatio-temporal variation in resources, size-dependent species diversity, and scaling biases in research techniques. Nevertheless, it is theoretically possible and practically desirable to use scaling methodology for predicting ecological requirements, for analyzing resource use and ecological time scales and for conservation purposes.

INTRODUCTION

Body size is an excellent predictor of many physiological and morphological characteristics of embryonic and adult birds (Paynter, et al. 1974, Rahn & Paganelli 1981, Calder 1984, Rahn et al. 1985, Walsberg 1987, Nagy 1987, Vleck & Vleck 1987). Allometric equations formulated from data derived from hummingbirds to ostriches have fostered considerable research by identifying general patterns and highlighting those species which do not fit the trends. The use of scaling on the ecological level has received much less study, but scaling is potentially useful for avian ecology in many ways:

- a) The most obvious use is simply to render the data manageable and to obtain empirical summaries. In a less than perfect situation, scaling allows pattern analysis of spotty but available data.
- b) A significant correlation arising from scaling is a generalization which might suggest sources of variation after factoring out body size.
- c) Predictions from scaling equations are first approximations for estimating ecological requirements, for designing experiments with species for which actual measurements are now missing, or for determining what reserve size is needed to prevent a species from extinction.
- d) Comparisons of allometric generalizations derived separately may suggest i) the ways in which internal function is adapted to environmental factors and community structure, and ii) how physiological capacity has responded to natural selection in the face of biotic and abiotic realities.

Notably and intentionally missing from the possible applications listed above is establishment of causality and theory. An existing bird is an outcome, an adaptive suite of form, function, and life history, for which we cannot deduce anything about the genetic basis of scaling of body proportions and life history variables. Ornithology has been

advanced considerably by documentation of patterns generated by least squares regressions (LSR) of log-transformed data on log body mass. The past decade focused on procedures: how we should measure size, which data we should include, which model of regression we should use. These debates provided valuable insight about statistics, taxonomic effects, and interpretations (Harvey 1982, Harvey & Mace 1982, Clutton-Brock & Harvey 1984, Smith 1984a,b, Bennett & Harvey 1987, Read & Harvey 1989. See LaBarbera 1989 for a provocative review). Prudence and caution dictate the need to refine statistical approaches. However, considerable effort may produce refinements which exceed that warranted, given the coarse nature of the original data, which tend to exclude valid but unpaired data, and which inhibit speculation and hypothesis formulation. Awareness of limitations to application should not preclude productive use of biological scaling techniques.

In this paper we explore aspects of the extent to which scaling might be fruitfully applied at the population or community level, which has considerably more variables than can invade the controlled environment of a laboratory.

METHODS

Body mass (m , in g) is the measure of body size in the scaling equation, $Y = a m^b$. We used one or an average value for each measured variable Y per species (n = number of species). The exponential scalings (b) were derived from log-transformed data. Least-squares regression (LSR, Model I) analysis yields a straight line with slope b , the proper form for predictive applications (Sokal & Rohlf 1981, pp. 547-549). LSR should be used with caution unless body mass is assumed to be an essentially error-free, independent variable. LSR and reduced major axis (RMA, Model II) scaling lines are identical when the correlation coefficient r is 1. As the correlation weakens, the two diverge. The RMA slope b is "the ratio of the standard deviations of points measured on the y axis and on the x -axis", s_y/s_x (Harvey & Mace 1982), while the LSR b is the product $r(s_y/s_x)$ (Snedecor & Cochran 1967). Therefore the RMA scaling exponent can be determined from the LSR as $RMA\ b = LSR\ b/r$.

RMA "assumes that error variance is the same proportion of the total variance on each axis, which may be closer to reality . . ." (Clutton-Brock & Harvey 1984) and has the least bias (Rayner 1985). However, ". . . both estimation of functional relationships and prediction are carried out best by means of simple linear regression, but when both variables are subject to error the appropriate method depends on the nature of the data... The subject of Model II regression is one which research and controversy are continuing and definitive recommendations are difficult to make. Much will depend on the intentions of the investigator." (Sokal & Rohlf 1981, pp. 547-549; see also Seim & Saether 1983). If preservation of biotic diversity is the concern and specific data are lacking, predictions [for which Model I or "least squares regression" (LSR) is best] may offer a first approximation.

Rising & Somers (1989) decided body mass was inferior to lengths or principle component analysis for expressing body size, on the basis of larger coefficients of variation (CV) for mass than for any of several linear measurements from a single species' body form. However, mass, like volume, is the product of three linear dimensions, so its CV would be expected to be compounded to about three times the

TABLE 1 – Correlation Strength and Level of Regression.

FUNCTION	SCALING	R	FUNCTION	SCALING	R
MAMMALS					
Body surface area	0.67 ^a	0.99	Home range area	1.02 ^b	0.93
Gut contents	1.05 ^{ch}	0.99	Fieldmet. rate	0.81 ^d	0.98
Metabolic rate	0.76 ^b	0.98	Population density	-0.78 ^e	-0.80
Max heart rate	-0.19 ^f	-0.99	Intrinsic rate of increase	-0.26 ^g	-0.69
BIRDS (ADULTS)					
Body area	0.67 ^h	0.998	Home range area	1.17 ⁱ	0.793
Resting metabolic Rate	0.67 ⁱ	0.99	Field metabolic Rate	0.64 ^d	0.95
Feather density	-0.27 ^k	0.905	Population density	-0.49 ^l	0.42
Lifespan in captivity	0.19 ^b	0.70	Lifespan in nature	0.20 ^{bs} 0.14 ^{i,G}	0.78 0.52
BIRDS (EGGS)					
Conductance to water vapour	0.81 ^m	0.97	Waterloss	0.75 ^p	0.93
Shell thickness	0.46 ^m	0.97	Incubation time	0.22 ^m	0.73
Pre-pipping O ₂ consumption	0.71 ^o	0.97			

Data in the right and left columns were collected in the field and laboratory, respectively.
Sources: ^a Peters 1983; ^b Calder 1984; ^c Demment 1983; ^d Nagy 1987; ^e Damuth 1987; ^f Baudinette 1978; ^g Henneman 1983; ^h Walsberg & King 1978; ⁱ Calder 1990b; ^j Bennett & Harvey 1987; ^k Welty 1982, Pettingill 1985; ^l Juanes 1986; ^m Ar &Rahn 1978; ⁿ Ar et al. 1974; ^o Hoyt & Rahn 1980; ^p Ar & Rahn 1980.
Qualifiers: ^H = herbivores; ^G = 215 longest-lived by genus; ^S = 152 longest-lived species.

average CV for a linear measurement. In fact, the CV for mass was less than such a value (Strauss & Calder MS). Lengths, judging from the diversity often represented in allometric regressions (e.g. duck to darter, *Anhinga*), would not likely predict metabolic requirements as well as masses do.

Examples of tightness of correlation, comparing r values from captive and field measurements, appear in Table 1. Damuth (1981,1987) reported that population densities of 467 species of mammals were proportional to M^{-0.78}, with r = -0.80. The scaling was similar in magnitude but opposite in sign from basal metabolism (M^{0.76}, r = 0.98) measured in laboratories. For birds, the difference in correlations for density and metabolism is more dramatic: r = -0.42 and 0.99, respectively, but such results are due to slope differences, (higher b giving higher r) and to scatter in the data. Body surface

areas of mammals and birds ($M^{0.67}$) correlate more tightly with body mass ($r = 0.99$) than is the case for land surface areas which they occupy (mammals: $r = 0.87$, birds: $r = 0.79$). Thus confounding variables could have a differential effect on RMA scalings, although this is not clear for many cases, perhaps due, in part, to effects of sample size and the fact that r is influenced by regression slope (r is equal to b divided by the complex denominator S_y/S_x). The residuals remind us that regression cannot tell it all – environmental adaptation and history have their influences.

The correlation coefficient (r) for scaling might be expected to decrease as ever more variables come into play as the scaling technique is employed from egg and bird to avian ecology. For example, there are natural spatial and annual variations in productivity with consequences for resource availability and carrying capacity, niche specialization, size- dependent species diversity, anthropogenic disruption, errors in measurement and calculation, seasonal hormonal states, and local adaptations.

Better correlations are often obtained by regressing life history variables on each other directly, bypassing body size (Partridge & Harvey 1988, Read & Harvey 1989, Harvey, this volume). However, in some situations or types of study, body mass scaling is still the most practical approach for dealing with:

- 1) Evolution and consequences of size (e.g. Bergmann's and Cope's rules, community and fossil assemblages) and first approximations to variables for species lacking actual measurements.
- 2) If not of primary interest, size is factored out via ratios of observed values to size-predicted values from general allometry, and
- 3) Limited data sets, too few species with data for both variables of interest: regressions can be run with species hypothetical A, B, C, D, and E (distributed over a good range in size) on mass for variable 1, and on species D-J on mass for variable 2. A ratio of scalings (Stahl 1962) in two or more regressions gives a first approximation to the relationship (see example of sound and area, below). This is, of course, compoundedly crude because of variances around both slopes (LaBarbera 1989), but central tendencies provide something more for thought than mere failure to find patterns through rigid adherence to ideal criteria which cannot be met with data presently available.

SCALING OF RESOURCE USE

Home areas

Space use and claims are important ecological characteristics of birds. Schoener (1968) found that territory scaled as the 1.09 power and home range as the 1.16 power of body mass. Adding nine territory sizes of other species from the literature does not change the basic scaling:

$$\text{area, ha} = 0.033 m^{1.17} \quad (1)$$

(m = mass, range 3.2 to 4500 g; $n = 86$; SE of $b = \pm 0.098$; $r = 0.793$; $F = 143.7$, $P < 0.0001$ Calder 1990a).

Reserve size and population size

Multiplying the area scaling by some number for minimum viable population size for species survival (e.g. the “500” of Frankel & Soule 1981) might be one “back of an envelope” approach to preliminary estimation of minimum reserve size:

$$500 \times 0.033 \text{ m}^{1.17} \quad (7)$$

This predicts a minimum of 244 ha for a hypothetical 10 g species, 3610 ha for a 100 g species, and 53,393 ha for a 1 kg species, estimates perhaps no more tenuous than the number 500 itself.

Song power output

Birds vocalize to claim space and resources, to warn intruders, and to attract mates. Singing conserves energy by reducing the need for flight and direct confrontation. Sound output power should have implications for ecology, behavioral energetics, and community structure. Direct correlation would be preferable, but with too few species with data on both home or territorial areas and sound outputs, separate body size regressions were necessary.

The relationship of milliwatts of sound output power (corrected to 1 m distance) to body mass (range 6 to 10800g) was:

$$\text{power output, mW} = 0.042 \text{ m}^{1.14} \quad (2)$$

(SE of b = + 0.084; F = 185.5, P < 0.001.). Body size accounts for 86.1% of the variability in sound output (r = 0.928; Calder 1990a).

The mass scalings for area (b = 1.17) and sound output (b = 1.14) are statistically indistinguishable (P > 0.25; F-test), so mass can be factored out by combining equations (1) and (2):

$$\text{sound (mW)/ area (ha)} = 1.28 \text{ m}^{-0.03} \quad (3)$$

Thus vocal capacity and spatial requirements appear to have evolved together, with a size independent of body size, resulting in a ratio of 1.3 mW of sound output at 1 m distance per ha.

The scaling of equation (2) can be used with the inverse square rule to calculate the radial distance from a song perch at which the intensity would fall to a minimal audibility, say 30 dB (20 dB is a whisper). Under “ideal” conditions (no attenuation or signal degradation due to wind, turbulence, or vegetation, in an environment completely free of sounds other than birdsong) the census taker with perfect hearing would hear a hypothetical 1 kg bird within a 4.2 km radius, while a hypothetical 10 g bird would have to be within 304 m to be heard. Thus, the area from which a census taker could hear all the less vociferous 10 g birds would be only 2 per cent of the area from which all 1 kg birds could be heard.

The Breeding Bird Survey was developed “to detect population trends within species from year to year” (Bystrak 1981). However, “species differ in how easy they are to see or hear, so the effective area sampled from a point or a line will differ between

species. Each species is therefore measured on a separate scale, and the counts of different species may not be added together or used in species-diversity calculations . . .” (Dawson 1981). Caution should be exercised in estimating population densities from transect censuses that depend heavily on calls and song.

Population densities

Much time and energy must be invested to obtain accurate population density data. Damuth (1981) combined allometries of herbivorous mammalian densities (D) and basal metabolic rates (E) to obtain a relationship for population energy requirements. Since the exponents were of opposite sign but numerically identical ($D = k M^{-0.75}$; $E = k M^{+0.75}$), the scalings canceled, suggesting that community net primary productivity (NPP) was apportioned independent of consumer size. This calculation overlooks probable biases of studying species that are more abundant in local distribution (Brown & Mauer 1986, 1987, Lawton 1989) and the fact that species diversity is inversely related to body size (more small species than medium-sized ones, and more mediums than large (Van Valen 1973, May 1978, Calder, 1984 p. 298, Brown & Mauer 1986, Lawton 1989). Scaling of D in birds is a much shallower inverse relationship with weaker correlations than in mammals (Peters & Wassenberg 1983, Juanes 1986, Brown & Maurer 1986). The product of these D s and basal metabolic scaling yielded positive exponents ($b > 0$), indicating that large birds consumed more of NPP than small species. These calculations overlook the additive effects when the environment is utilized at a finer grain by a greater number of species in smaller body size ranges (Maurer & Brown 1988, Lawton 1989). For example, in the compilation of North American bird weights (Dunning 1984), more than half (57%) are under 100g, a weight that is 8% of that of the largest passerine and under 1% of the largest non-passerine.

Lawton (1989) argued “. . . it is impossible to say what the real relationship between population density and body mass is; or rather what the relationships are . . .”. He distinguished between upper and lower bounds in and to scatter plots of log density vs. log body size, and pointed out that conclusions about per capita use of resources were based on upper bounds, the scaling of which would be valid only if the lower bounds were parallel. Another matter of concern is that density and diversity tend to fall off from the inverse trend at the small end of the size range within a class or smaller grouping (Dial & Marzluff 1988, Maurer & Brown 1988).

We feel it is premature to abandon examination of density/size relationships before adequate true densities are available. It seems desirable that we explore further and improve knowledge of such bounds with awareness of errors that could come from improper interspecific use of linear transect counts pointed out above. Since spatial scales (environmental grain) are perceived in a size-dependent way, ecological density is based on area of intense use. The reciprocal of home range or territory has the dimensions of D [$1/(\text{area/bird}) = (\text{birds/area})$], and thus better approximates ecological density. It is dimensionally correct for birds that are dispersed in space (not flocked or colonial, seasonally or by nature). While this overlooks the existence of “floaters” or birds who have not succeeded in staking territorial claims, so do linear transects that utilize only the conspicuous songs, posting, and activities associated with ownership:

$$D = 1/0.033 \text{ m}^{1.17} = 30.3 \text{ m}^{-1.17} \quad (4)$$

The field metabolic rates (FMRs) of birds (Nagy 1987) are scaled:

$$E = 10.9 m^{0.64} \quad (5)$$

This is similar to an earlier derivation by Walsberg (1983):

$$E = 13.1 m^{0.61} \quad (6)$$

The products, DE , scale as $m^{-0.53}$ to -0.56 . Smaller, but still negative exponents are found when passerine and non-passerine birds are analyzed separately (passerine -0.35 ; nonpasserine -0.08). When analysis is limited by phylogeny, the smaller range in bird sizes used in the analysis reduces the strength of correlation.

Hence it may be that small birds take more, not less than the large, of the NPP, particularly if the size-dependency of species diversity is taken into account. Avian community partitioning of NPP deserves further study, but a better data base of true population densities is probably a prerequisite for success in this.

ECOLOGICAL TIME SCALES

A life history is comprised of many time periods. They scale with the following mass exponents: from heartbeat to heartbeat (0.23), incubation (0.20), fledging time (0.18 to 0.20), sexual maturity (0.23), life expectancy (0.46), and maximum lifespan (0.14 to 0.20) (Calder 1984, 1990b). We will examine scaling relationships which bear on two major emphases of ecology: foraging and reproduction.

Digestion time

Karasov et al. (1986) showed that periodic cessation of foraging activity by energy-maximizing hummingbirds could be due to limitations in rate of digestive processing. Determination of gut passage or retention times is complicated by differences in passage of solids varying in digestibility, laxitivity, and fluid components of the diet. Owing to paucity of measurements these distinctions are ignored to make a first approximation of the scaling of gut transit time from intake to first appearance of stained material in the faeces (Figure 1):

$$\text{"gut passage time", min.} = 23.7 m^{0.31} \quad (8)$$

[$n = 36$ species, 3.5 to 38,000 g; $r = 0.751$; $F = 43.90$, $P < 0.005$; SE of $b = 0.046$; data from Gasaway et al. (1975), Walsberg (1975), Sturkie (1976), Herd & Dawson (1984), Herrera (1984), Karasov et al. (1986)]. This scaling exponent is statistically indistinguishable from the scaling ratio for gut size/metabolic rate in birds, and from the 0.28 to 0.30 derived for ruminant and nonruminant mammals (Demment 1983, Demment & Van Soest, 1985). Such scaling is consistent with the apparent lower size limit for microbial fermentation of crude fibers (a minimum of 2 h for the 425 g ptarmigan *Lagopus mutus*), indicative of size constraints on food habits and feeding behavior. Rapid digestibility, not energy density (J/g wet), is the primary consideration in the diet of very small birds; grass is about as rich (J/g) as the average floral nectar.

Longevity

Maximum longevity (t_{max}) scales with a somewhat smaller body mass exponent than the 1/4 scaling of metabolic turnover and other physiological and life-history scalings (Calder 1984). Lindstedt & Calder (1976) suggested that avian t_{max} data could have been biased by the fact that small birds with shorter lifespans had been more extensively sampled in the few decades of banding and recaptures than large birds.

Klimkiewicz & Futcher (1989) extracted t_{max} records of 498 species of wild banded birds from the computer files of the US Fish and Wildlife Service Bird Banding Laboratory, through 1987. Limited sample sizes contributing the oldest records probably understate considerably the ages actually attained for each species. Typically less than 10% of banded birds are subsequently recaptured, collected, or found dead, except for colonial-nesting marine birds, and hunted species of fowl, waterfowl, and doves. Intense banding/recapture efforts are necessary to obtain longevity records which actually reflect life's limits. Attempting to eliminate the understudied, Calder (1990b) used only the maximum longevity within each of 215 genera represented. Mass from Dunning (1984) accounted for 27% of variance:

$$t_{\text{max}}, \text{ years} = 5.45 m^{0.14}$$

(9)

GUT PASSAGE TIMES OF BIRDS

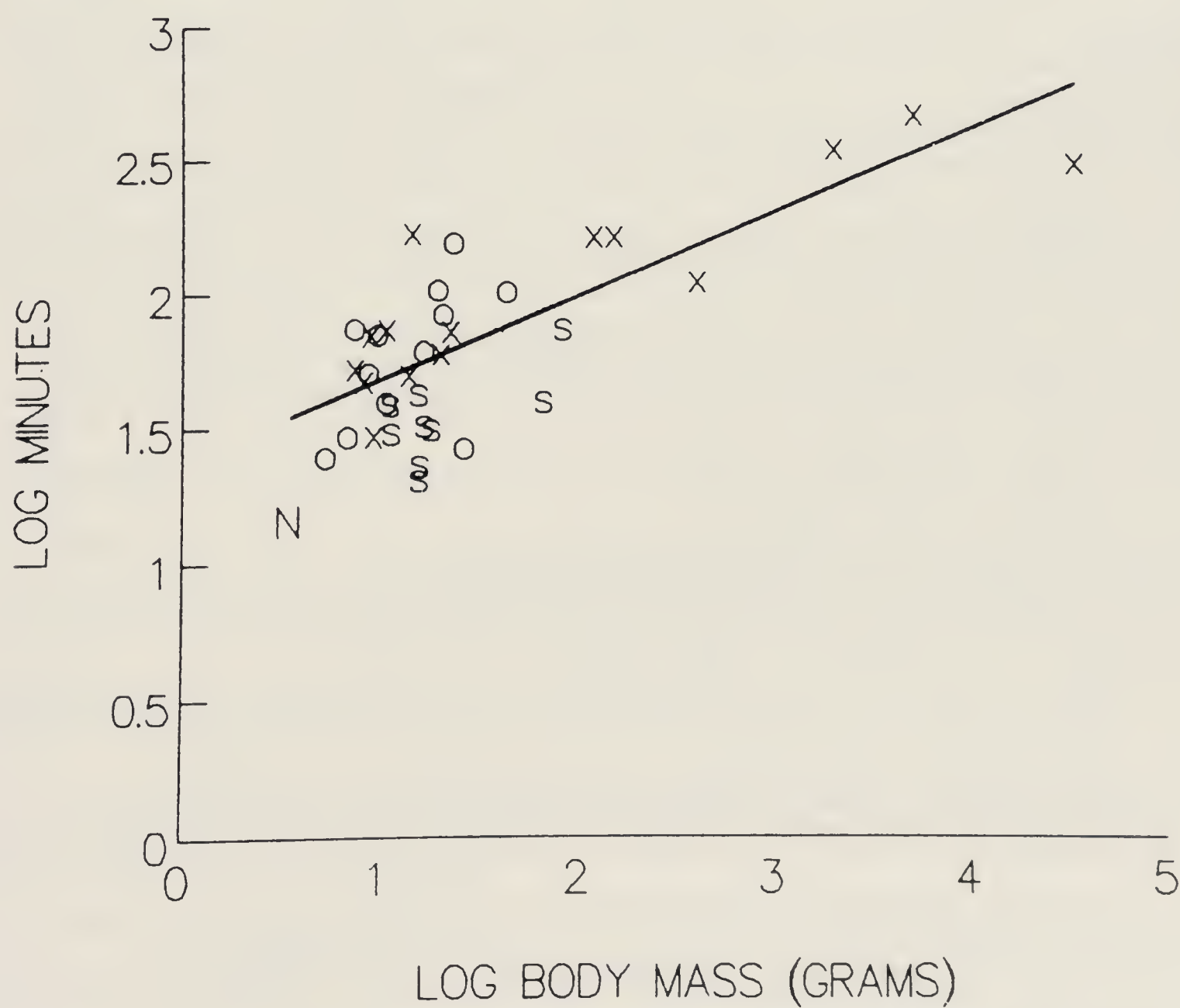


FIGURE 1 – Times for passage of ingested food through bird digestive tracts. N = nectar-feeder, S = seed-eater, O = frugivore, X = other non-frugivore.

($r = 0.518$, $P < 0.001$, SE of slope 0.016). This predicts shorter t_{\max} for all birds over 33g in body mass, compared to Lindstedt & Calder's (1976) equation for wild birds.

Total numbers of bandings from which the records could have been sampled, as reported for 192 of these species by Clapp et al. (1982, 1983) and Klimkiewicz et al. (1983, 1987) were regressed as log number of bandings per species vs. log body mass to check for any systematic bias towards smaller birds, more likely to be caught by back-yard banders. The correlation between banding frequency and bird size was weak and statistically insignificant ($r = 0.014$). Similarly, t_{\max} did not correlate significantly with number of birds banded ($r = 0.038$). Hence, we have no explanation for why these t_{\max} scaling exponents are consistently less than 1/4. The addition of over two decades' worth of captive mammal and wild bird longevity records has not shown a significant t_{\max} increase, suggesting that we may be approaching a point of diminishing returns in derivation of t_{\max} scaling.

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BODY SIZE AND FORAGING BEHAVIOUR IN BIRDS

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ABSTRACT. Foraging time in birds is an inverse function of body size. All else being equal, smaller species must spend more time feeding because of higher metabolic demands on a gram per gram basis (Kleiber's rule). This can limit the flexibility of small species to adjust activity budgets to fluctuations in food abundance or environmental conditions. As well, greater energy reserves of larger species can promote a strategy of "deferred foraging" to await better environmental conditions. Selection for large body size would appear to be an evolutionary force in harsh (cold) environments (Bergmann's rule).

Keywords: Body size, time budgets, allometry, feeding behaviour, Kleiber's rule, Bergmann's rule.

INTRODUCTION

The relationship between metabolic rate and body size in birds follows Kleiber's 3/4 rule ($\alpha M^{0.75}$, where M=mass; Kleiber 1961, Calder 1984). This well-known allometric relationship results from the thermodynamic consequences of body size. On a gram per gram basis, small animals must maintain a higher metabolism than large animals to compensate for greater heat loss to the environment (Peters 1983). Empirical data reveal that ingestion rates for birds and other taxa are similarly scaled with body size ($\alpha M^{0.63}$ - $M^{0.84}$, Peters 1983, Calder 1984) — presumably because metabolic rate largely determines food requirements. The volume of the digestive system of birds (gut capacity), however, is a linear function ($\alpha M^{1.0}$) of body size (Quiring 1950, Calder 1984). Thus, energy demand (daily consumption) is greater on a gram per gram basis for small birds than for large ones — but the maximum amount of food able to be consumed on any foraging trip is scaled linearly with body size.

From these considerations, one can calculate (Calder 1984) that daily consumption divided by gut capacity equals the frequency of foraging trips required to obtain food — which should be approximately proportional to $M^{-0.25}$. However, predators vary considerably in their modes of foraging and in the size and quality of prey consumed. Empirical data on "killing rates" (ingestion rates divided by prey size) indicate that frequency of foraging in homeotherms is proportional to $M^{-0.49}$ (Peters 1983). In any case, the data indicate that small birds must spend more time foraging than large birds. This constraint has important ecological consequences for birds, especially in harsh environments (Goudie & Ankney 1986).

FIELD STUDIES OF FORAGING ACTIVITY BUDGETS

There have been relatively few studies of feeding time budgets in multi-species feeding guilds (Calder 1974). In his classic study of tits (*Parus* spp. and *Aegithalos*

cauclatus) and the Goldcrest *Regulus regulus*, Gibb (1954) found that the proportion of time spent feeding by each species was inversely related to body size for these 5g to 18g passerine insectivores. This trend was most conspicuous in fall and winter, when birds were most active and food was least abundant (Figure 1). The largest species (Great Tit *Parus major*) spent between 59% and 81% of its time foraging in the months of September to March, whereas the tiny Goldcrest was foraging 88-100% of the time it was observed in those months. Blue Tits *P. caeruleus* and Marsh Tits *P. palustris* are both about the same size (ca. 10g), but Marsh Tits consistently spent more time foraging than Blue Tits. This departure from the general body size trend may be explained by differences in foraging behavior between the two species (see also below). Blue Tits concentrated their foraging in relatively few productive habitats, whereas Marsh Tits were more widely dispersed in a greater variety of foraging habitats. Despite this added component of variation, body size still explained 92% of the variation between species in winter feeding activity and time spent feeding was proportional to $M^{-0.25}$ in this feeding guild (Figure 2).

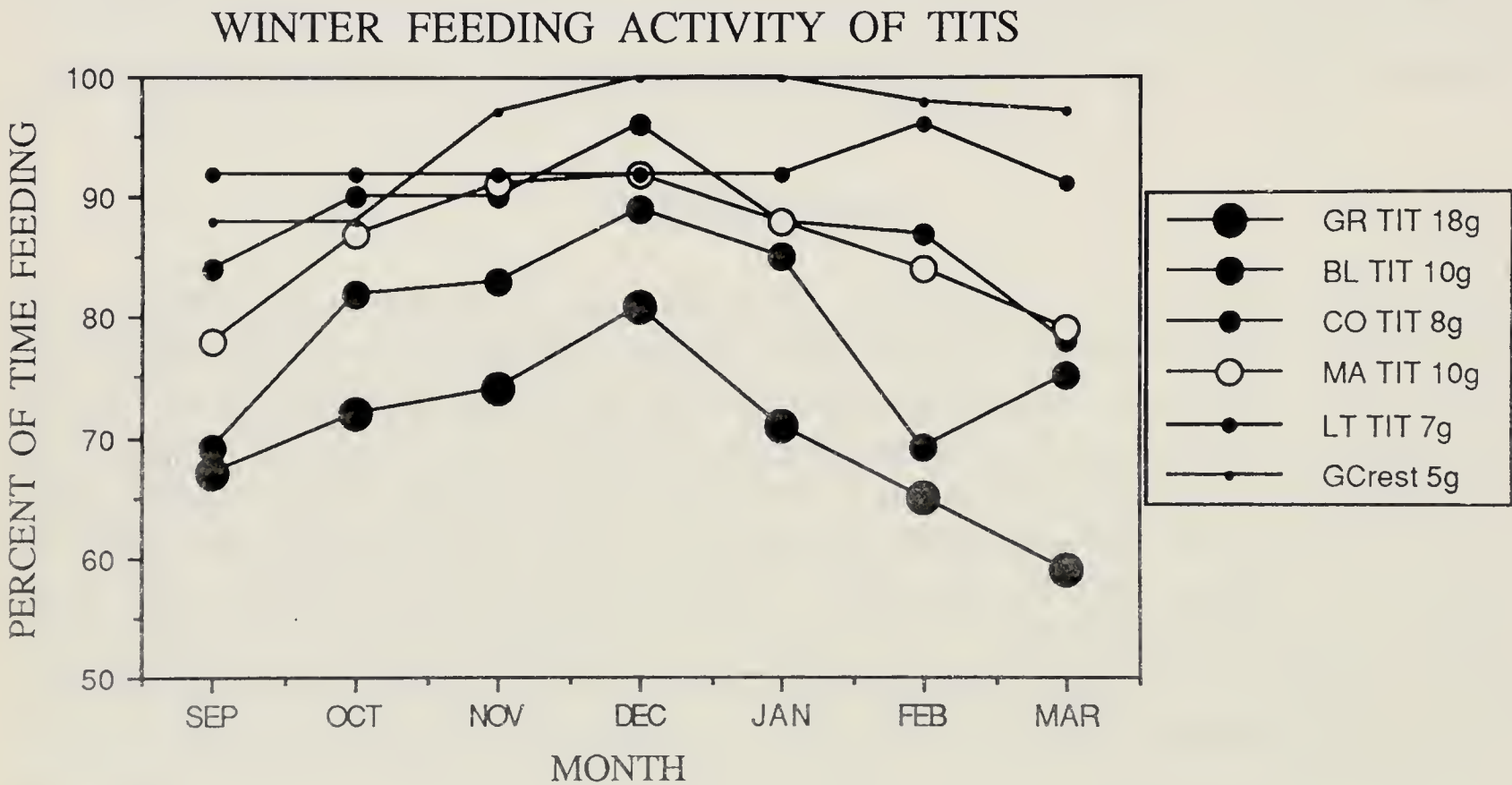


FIGURE 1 - Activity time budgets of tits in winter. Compiled from Table 3 in Gibb (1954) for the months of September to March. Species codes: GR TIT - Great Tit *Parus major*; BL TIT - Blue Tit *P. caeruleus*; CO TIT - Coal Tit *P. ater*; MA TIT - Marsh Tit *P. palustris*; LT TIT - Long-tailed Tit *Aegithalos caudatus*; GCrest-Goldcrest *Regulus regulus*.

Pearson (1968) studied the feeding ecology of eight coexisting seabirds at the Farne Islands, Scotland. Species ranged 17-fold in size from Arctic Terns *Sterna paradisaea* (104 g) to Shags *Phalacrocorax aristotelis* (1785 g) and included surface-feeders (terns, gulls) and divers (alcids, shags). Dietary overlap between species was high and most fed on small forage fishes (77-100% of diet) ranging in length from 25 to 150 mm. For each species, Pearson calculated the percent of daylight hours spent in fishing activities that would be required for adults feeding one chick — or for those species with multi-egg clutches (terns, gulls, shag) — several chicks. Regression of those data (Figure 3) indicate that feeding frequency is proportional to $M^{-0.81}$ - $M^{-0.86}$ in this feeding guild and that body size accounts for 81-91% of the variation in feeding frequency. Shags required as little as 4-8% of daylight hours to feed chicks, whereas

Arctic Terns had to forage over 100% of the day to rear two chicks. The scaling constant is considerably lower in this feeding guild than predicted or observed elsewhere (e.g., $M^{-0.25}$ - $M^{-0.49}$). This is possibly because time spent feeding included time spent by adults foraging for themselves, foraging for chicks, and for delivery of food back to their chicks; so that whatever time advantage the larger species gained was multiplied several-fold. Also, foraging time may have been underestimated for some of the larger species (e.g., Common Murre *Uria aalge*, Burger & Piatt 1990).

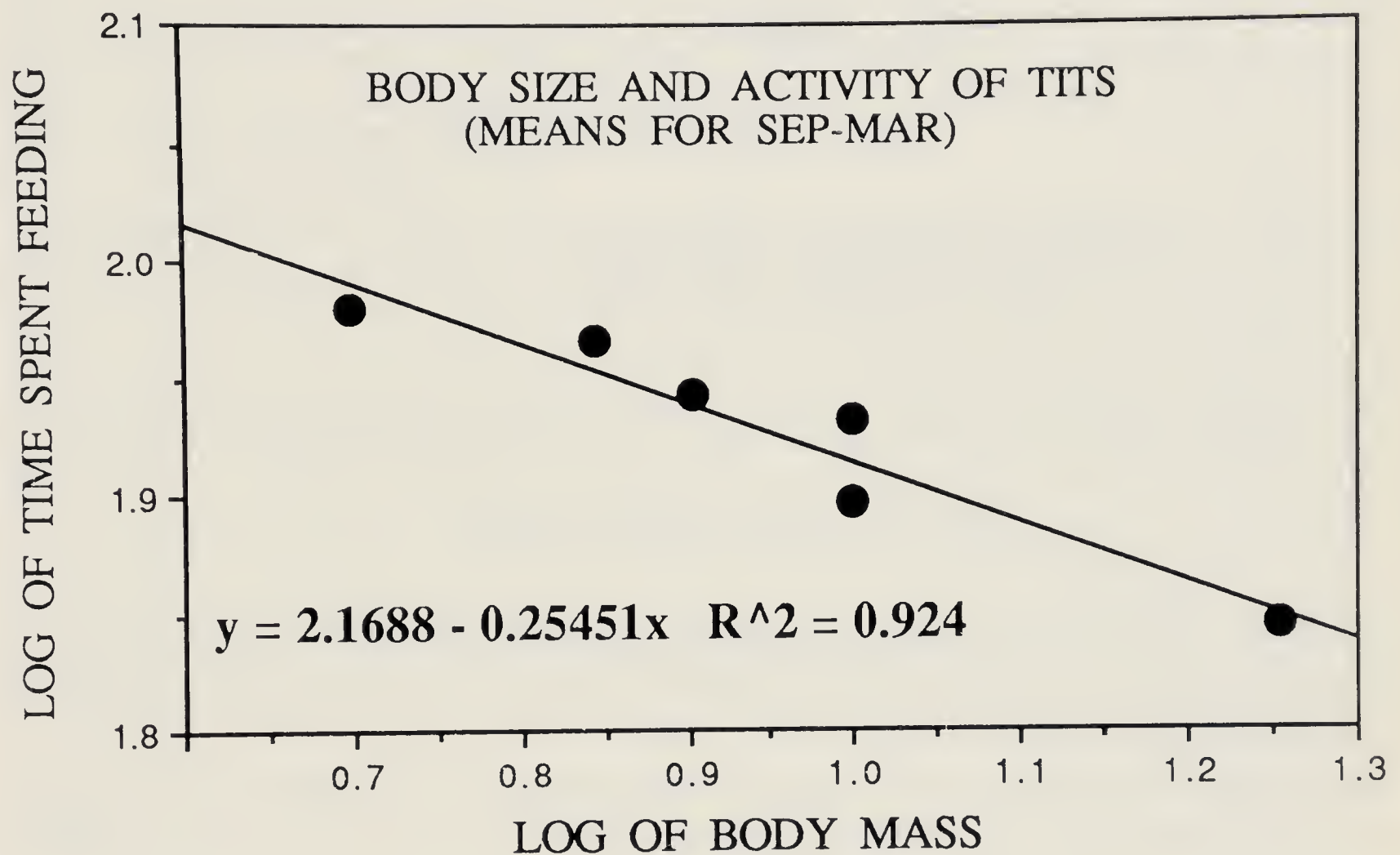


FIGURE 2 - Regression of (log) time spent feeding by tits versus (log) body size (g). Data from Gibb (1954). See Figure 1.

Finally, Goudie & Ankney (1986) studied the winter feeding ecology of four coexisting species of sea-ducks in Newfoundland. Body sizes ranged about three-fold from Harlequin Duck *Histrionicus histrionicus* (610 g) to Common Eider *Somateria mollissima* (1790 g). Differences in quality of food and choice of foraging habitat probably influenced feeding rates (e.g., Harlequin Ducks tended to dive in shallower water and on prey with higher energy density), but body size still accounted for 53% of the variation in time spent feeding — which was proportional to $M^{-0.28}$.

Whereas the empirical and theoretical evidence suggest that body size accounts for most of inter-specific variation in time spent feeding, foraging behaviour (style) probably accounts for much of the residual variation (see also Nagy & Obst; this symposium). The importance of behaviour in foraging energetics and activity budgets has been documented best in lizards — which range in behaviour from those that “sit-and-wait” in isolation to opportunistically consume dispersed prey, to those that “widely-search” in large groups for dense prey aggregations (Huey & Pianka 1981). Daily energy expenditures in widely-searching species appear to be about 1.3-1.6 times greater than in sit-and-wait predators, but the extra effort pays off because gross food intake may be twice that achieved by sit-and-wait predators (Huey & Pianka 1981).

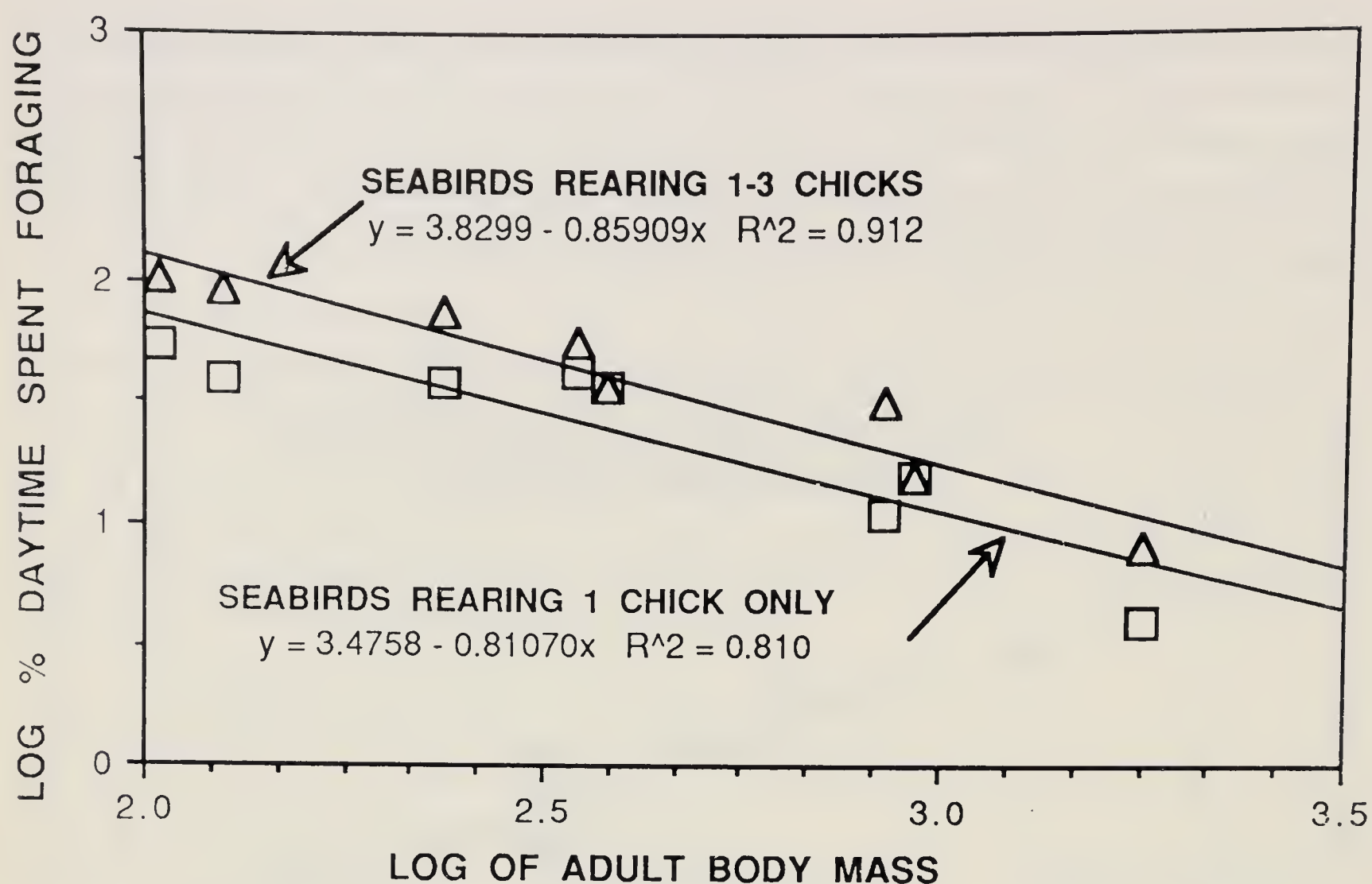


FIGURE 3 - Regression of (log) time spent feeding by seabirds versus (log) body size (g) for seabirds rearing 1 chick (squares) or seabirds rearing 1-3 chicks (triangles). Data from Pearson (1968). See text for details.

Furthermore, widely-searching species may spend two to three-fold less time foraging than similarly sized sit-and-wait species because high density prey aggregations, when found, can be rapidly exploited (Nagy et al. 1984). Although less well documented, it appears that within most feeding guilds of birds there are behavioural equivalents to the "sit-and-wait" and "widely-searching" types of species found in lizard communities. Within foraging guilds whose members exhibit similar morphology and foraging styles, however, it appears that body size is the predominant factor influencing feeding frequency (Goudie & Ankney 1986, Piatt 1987).

ECOLOGICAL IMPLICATIONS

In harsh environments, small species have little flexibility to adjust their activity budgets because most of the day is spent seeking food [e.g. Nilsson 1970 for Common Goldeneye *Bucephala clangula* and Oldsquaw *Clangula hyemalis*; Pearson 1968 for terns (*Sterna* spp.); Goudie & Ankney 1986 for Harlequin Duck and Oldsquaw]. Furthermore, starvation is a more imminent threat to relatively small species. Survival time for birds in thermally neutral environments is proportional to $M^{0.26}$, and survival time for passerines at 0°C scales to $M^{0.47}$ (Peters 1983). Thus, large birds take longer to starve than small birds, and small birds are more adversely affected by cold temperatures than large birds. For example, Common Eiders could survive 40% to 50% longer without food than Harlequin Ducks (Goudie & Ankney 1986). King Penguin chicks *Aptenodytes patagonica* (ca. 5-7 kg) can tolerate fasts of four to six months

and a 70% decrease in body mass (Cherel et al. 1987). In contrast, Dippers *Cinclus cinclus* are relatively small (50-70 g), and fat reserves allow only four to six hours survival in winter without food should their open-water habitat freeze over (Lehikoinen & Hakala 1988). Golden-crowned Kinglet lipid and food reserves can support individuals for less than a day in winter (Blem & Pagels 1984). Hummingbirds must spend most of the day actively foraging just to exist, and added stress from rain or cold temperatures may cause them to enter a nocturnal torpor in order to conserve energy reserves overnight and compensate for lost food intake during the day (Hainsworth et al. 1977, Calder 1974). Between-sex differences in energy reserves have also been demonstrated for species exhibiting sexual size dimorphism — which would confer some advantage in winter to the larger sex [e.g., Common Goldeneye (Nilsson 1970); Capercaillie *Tetrao urogallus*, (Gjerde & Wegge 1987)].

The differential ability to deal with increasing energy stress may result in differing foraging strategies for large and small birds. Nilsson (1970) and Goudie & Ankney (1986) demonstrated that the Common Eiders decreased feeding intensity with decreasing ambient temperatures, a strategy also noted for the Svalbard Rock Ptarmigan *Lagopus mutus hyperboreus* (Stokken et al. 1986) and Snow Geese *Anser caerulescens* (Frederick & Klass 1982). Thus, large species may defer foraging under extreme conditions to avoid wasting energy — a strategy that works as long as energy reserves permit. In contrast, smaller species may have to increase feeding intensity with decreasing temperatures [e.g. Nilsson (1970) for Goldeneye, Jorde et al. (1984) for Mallards *Anas platyrhynchos*], or when stressed for food [e.g. White-crowned Sparrows *Zonotrichia leucophrys* (Ketterson & King 1977)]. Within limits, the response of a bird to increased energetic demands is directly affected by the quality and quantity of food available. For example, Black Ducks *Anas rubripes* may increase or decrease feeding in winter depending on food quality (Brodsky & Weatherhead 1985).

The greater flexibility of time budgets in large species may also help breeding birds buffer against seasonal fluctuations in food supply. Burger & Piatt (1990) studied the activity budgets of Common Murres rearing chicks at a colony in Newfoundland over four consecutive breeding seasons. Local prey abundance varied 10-fold within seasons and between years, but this was not reflected in chick meal delivery rates or overall breeding success. Instead, adult Murres compensated for fluctuations in prey abundance by adjusting their foraging effort. Common Murres are the largest member of the alcid family of seabirds, and therefore probably have the greatest ability to buffer against fluctuations in food abundance (Piatt 1987).

CONCLUSIONS

Large birds have greater flexibility than small birds to adjust time budgets under harsh environmental conditions or during periods of food stress. On the other hand, they must extract an overall greater biomass of food from their environment. Small birds are forced by energetic demands to forage more frequently, and to search for higher quality prey — but they can subsist on a lower overall density of food. Therefore, small birds are more vulnerable to extreme environmental conditions, but may be able to exploit a greater variety of habitats. These factors may explain some patterns of species distribution, and geographic variation in body size within species. Within feeding guilds, small species may winter in areas with warmer ambient temperatures. Within

species, large body size may be selected for in cold, northern environments (Bergmann 1847).

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POSITIVE CORRELATION BETWEEN RANGE SIZE AND BODY SIZE: A POSSIBLE MECHANISM

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ABSTRACT. Empirical studies have shown that range size often correlates positively with body size (e.g. Brown & Maurer 1989). Factors influencing this relationship include: (1) increased environmental variability with bigger ranges, and (2) increased ability of larger species to maintain homeostasis under various conditions. In a select group of wintering North American passerines, larger birds were found to extend their ranges farther north than smaller species. The fat available at dawn for one of these species, Northern Cardinal *Cardinalis cardinalis*, was sufficient to maintain a metabolic rate of 2.5 times basal for 11.1 ± 1.8 hours in Tennessee and Indiana, but only for 4.0 ± 2.1 hours in Michigan. Therefore, at the northern range limit, Cardinals were close to their maximal ability to maintain thermal homeostasis. This suggests that the positive correlation between range and body size is partly due to direct relationships between body size and homeostatic variability, this variability and environmental variability, and the latter variability and range size.

Keywords: Homeostasis, environmental variability, geographic variability, thermogenesis, birds, Northern Cardinal, *Cardinalis cardinalis*.

INTRODUCTION

Many studies have empirically shown a positive correlation between range size and body size within specific taxa (e.g. Averill 1933, Van Valen 1973, Reaka 1980, Brown 1981, Brown & Maurer 1989). Mechanisms causing these patterns are not known. However, larger bodied animals, in general, have an ability to maintain homeostasis over a wider array of conditions than smaller bodied ones, and larger geographic ranges of species generally encompass more environmental variability than smaller ranges (Figure 1). Species with small body sizes, in contrast, will not be able to maintain homeostasis over a diversity of environmental conditions, resulting in local extirpations in more extreme environments. Consequently, their ranges will be reduced in size. Large bodied animals can easily maintain homeostasis over a small range, but the energy needed to maintain their large body sizes would require that food within the small ranges be of high quality and quantity. Such situations are rare, and when they do occur species' abundances will generally be low, making extinction probable (Rabinowitz 1981). Therefore, based on homeostatic ability and environmental variability the expected pattern is one of direct association between range size and body size (Figure 1).

If homeostatic ability and environmental variability are indeed defining the pattern, then many environmental factors could be structuring such a pattern. Ambient temperature is one that could be easily observed (Root 1988b); range edges would be limited by maximum thermogenic ability.

To investigate this possibility I compared different energy-storage and energy-utilizing variables across the winter range of the Northern Cardinal *Cardinalis cardinalis*

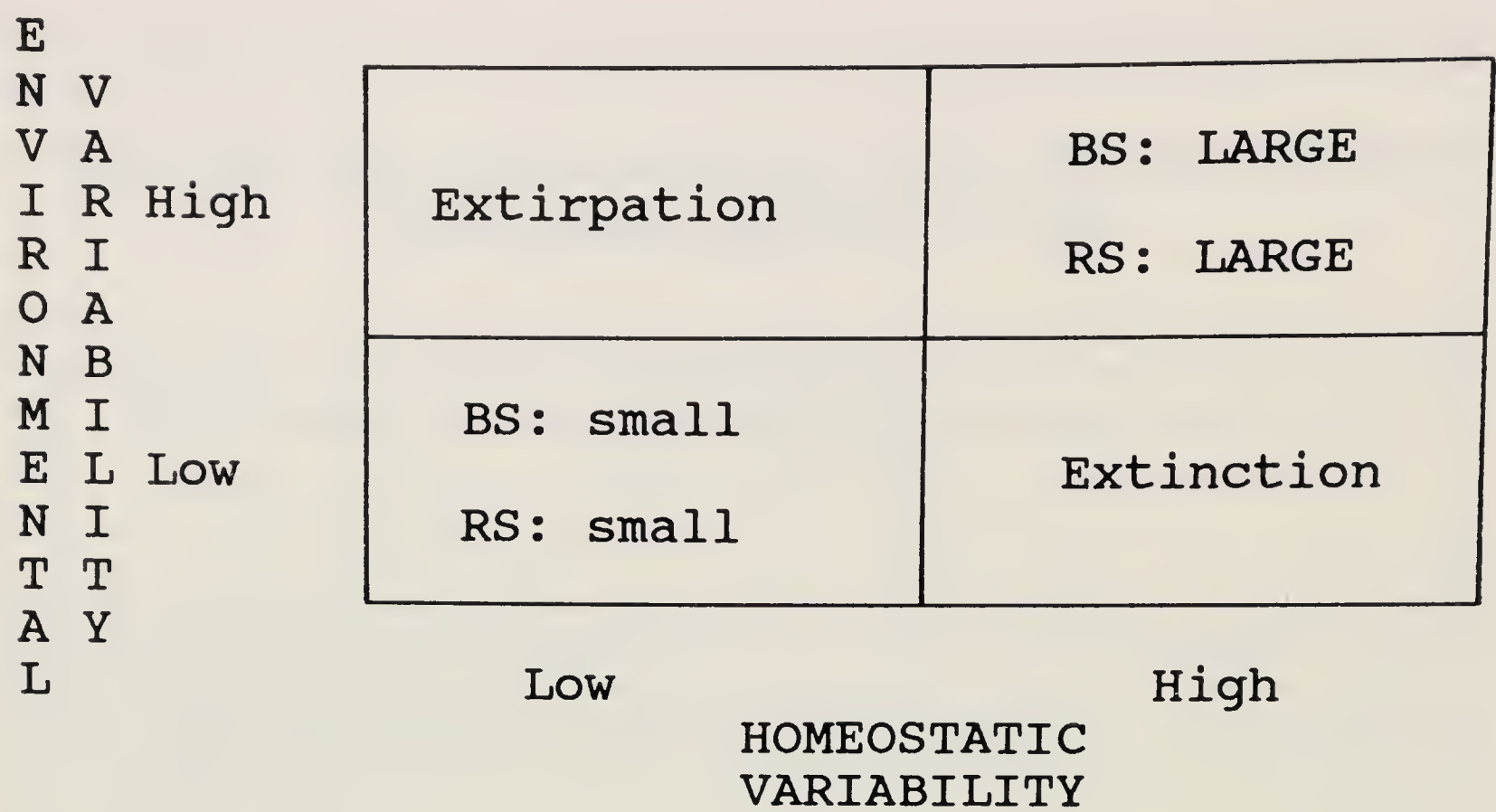


FIGURE 1 – Matrix of possible outcomes for body size (BS) and range size (RS) in environments with low and high variability, and species with low and high homeostatic variability.

to determine if energy availability restricts its northern range boundary. Energetic constraints could be manifest in several ways. First, the latitudinal increase in depot fat may not be sufficient to compensate for the latitudinal increase in energetic demands of thermogenesis. This could be due to a limited abundance of food, or not enough foraging time due to a latitudinal decrease in day length. Second, depot fat cannot be metabolized quickly enough to fuel the necessary thermogenesis.

In this study I examined geographic variation in metabolic rates, fat content, and fat-metabolizing enzymes of four populations of Cardinals across their winter range. The goal of this study was to determine if any of these physiological properties constrained this species from expanding its range into colder habitats.

OBSERVED PATTERN

In a previous study (Root 1988a), I found that metabolic rates at northern range boundaries (NBMR; $\text{kJ} \cdot [\text{bird} \cdot \text{day}]^{-1}$) of fourteen passerines were positively associated with body mass (M measured in g) when both variables were logarithmically transformed. The resulting regression equation was:

$$\log(\text{NBMR}) = \log(4.06) + 0.92 \log(M),$$

(1)

which has $r^2=0.87$. A reduced major axis analysis of $\log(\text{NBMR})$ and ambient temperature resulted in the following equation:

$$\log(\text{NBMR}) = 1.54 - 0.031 T,$$

(2)

where T is ambient temperature (average minimum January temperature in °C;

$r^2=0.71$). By combining equations (1) and (2), the following predicted relationship between body mass and ambient temperature was obtained:

$$T = 30.05 - 29.68 \log(M).$$

This equation was based on fourteen species, whose northern range boundaries were associated with a particular isotherm and for which winter physiological data were available. Values for thirty-six other species that had northern range boundaries associated with particular isotherms but for which no physiological data were available, also fit this line (Root 1988b; Figure 2). Consequently, for these select species, larger bodied birds have ranges extending farther north than smaller species. This suggests that the general pattern of range size correlating positively with body size may be partly due to larger species possessing the capability to maintain thermal homeostasis in a wider variety of habitats.

MATERIAL AND METHODS

I examined populations of Cardinals along a 1250 km transect that spanned the longitudinal length of its winter range in eastern North America. Individuals were captured at four transect locations from December 15 to February 28 in 1987/1988, 1988/1989, and 1989/1990 (hereafter referred to as 1988, 1989, and 1990, respectively). These sites included Ann Arbor, Michigan (MI; 42° 3'N, 83° 36'W), Bloomington, Indiana (IN; 39° 12'N, 86° 30'W), Smyrna, Tennessee (TN; 36° 0'N, 86° 24'W), and Eufaula, Alabama (AL; 31° 42'N, 85° 6'W). Birds were collected during the two-hour period before sunset.

Metabolic tests

A flow-through respirometry system was used to measure oxygen consumption in 1990. Within an hour of dusk, individuals were weighed and placed in an 1800 ml pressure-sealed metal chamber with air input and output ports. The chambers were painted flat black. Birds stood on a wire-mesh platform at the bottom of each can. Chambers were immersed in a bath of water and ethylene glycol. The bath temperature was preset to either 25°, 23°, -3°, or -8°C. Air dried with Drierite was supplied to each chamber at a regulated flow of 900 ml*min⁻¹. The birds were maintained undisturbed for at least four hours before their metabolic rates were monitored. Output air from the chamber was dried again with Drierite and the CO₂ removed with Ascarite before the oxygen content was measured using a portable paramagnetic oxygen analyzer. Standard metabolism values were determined by finding the minimum 10-minute average of metabolic values calculated using methods described in Withers (1977).

Conductance (C; J*[g*h*°C]⁻¹) was determined using

$$C = H / (T_b - T_a),$$

where H is metabolic rate in J*(g*h)⁻¹, T_b is body temperature in °C and T_a is ambient temperature in °C. Only metabolic rates recorded at -3° and -8°C, which are well below thermal neutrality, were used to calculate C.

Body temperature, which was recorded at the end of trials, was determined within a minute of initial disturbance of the bird by inserting a thermocouple approximately 1 cm into the cloaca of the subject. The body temperature of every individual was not recorded; I ran more than one subject each evening and the removal of the first potentially disturbed the others.

Only males were used and metabolic tests were run on the day of capture. Subjects were weighed to the nearest 0.01 g before the test. Individuals were sacrificed after removal from their chamber. They were weighed to the nearest 0.01 g.

Stored Fat

Fat was extracted from these sacrificed birds. Their guts were assumed empty because they had sat in metabolic chambers for a minimum of 5.5 hours.

Each specimen was lyophilized to a constant weight. The carcasses, with feathers intact, were then cut into pieces 1 cm³ or smaller. Neutral lipids were extracted using petroleum ether in a Soxhlet extraction apparatus. When complete, the residual ether was evaporated by heating at 80°C for 0.5 hr. After cooling, the lean, dry mass was determined. The difference between total-body dry and total-body lean, dry mass provided mass of the neutral lipids to the nearest 0.01 g.

Enzyme Assays

The activities of two different fat-metabolizing enzymes in the flight muscles were examined: citrate synthase (CS) and betahydroxyacyl-CoA dehydrogenase (HOAD). In 1988 birds collected for these assays were humanely sacrificed and within five minutes of death carcasses were frozen in liquid nitrogen. Birds collected in 1989 were humanely sacrificed, the left pectoralis muscle removed, placed in a Nunc tube, and frozen in liquid nitrogen within 30 minutes of death. The 30 minute lag time presumably had no influence on the enzyme activity (Root and O'Connor unpublished data on House Sparrows *Passer domesticus*).

While being kept on ice in the laboratory, approximately 0.25 g of pectoralis muscle was finely minced. This was then added to 10 volumes of homogenizing buffer containing 100 mM phosphate and 2 mM EDTA at a pH of 7.3 at 5°C. Homogenization occurred in a hand-held, glass-glass tissue grinder that was maintained on ice. Homogenates were sonicated three times for 15 s at 45 s intervals. The assay protocols from Marsh (1981) were followed and duplicate assays were run. Maximum activity values for each bird were averaged at each location.

RESULTS

Body Temperature

A regression analysis showed that body temperature was not dependent on ambient temperature ($r^2=0.047$), and consequently a mean value of $39.26 \pm 0.18^\circ\text{C}$ ($n=13$) was used.

Metabolism

Student's t-tests for small samples revealed no significant differences in the mean conductance values, and thus, these data were combined (2.22 ± 0.04). This value

was used as the slope of a line relating metabolic rate (H) with ambient temperatures (T) below the lower critical temperature. The principles of Newtonian cooling, which apply due to the independence of body and ambient temperature, require that this line pass through the point at which metabolic rate is zero and ambient temperature equals body temperature. The resulting equation is:

$$H = 87.16 - 2.22 T.$$

Metabolic rates above 23°C at each location were averaged to calculate BMR values. Student's t-test for small samples revealed no significant difference in mean values from IN and TN ($P=0.38$). The mean of these two states (60.04 ± 1.36) was found to differ significantly from that in MI ($P=0.04$) and approached significance with the AL mean ($P=0.07$). The difference between MI and AL was highly significant ($P=0.006$).

Stored Fat

Fat content of birds at dusk was estimated from individuals used in metabolic tests. During these tests they were held a known length of time in a metabolic chamber at a constant temperature. The estimated amount of fat used during these tests (F measured in g) was derived by the following equation:

$$F = M * K * t,$$

where M is standard metabolism in $J^*(bird \cdot h)^{-1}$, K is a conversion factor ($37.7 kJ=1g$ of fat; see Blem & Shelor 1986), and t is time in the chamber. To approximate the amount of fat available at dusk, F can be added to the amount of fat extracted from the individual carcasses (Table 1). This provided only a rough estimate of absolute fat content, because birds use digestive heat in the early evening to supplement thermogenesis (King 1972), and the minimum 10-minute average was the assumed metabolic rate for the entire trial. These estimates, however, allow comparisons among locations, because methods were constant across all locations.

Available Energy from Stored Fat

Due to the geographic scale of this study, the amount of depot fat available at dusk is not important for comparative purposes because influencing factors, such as night length and ambient temperature, vary latitudinally (King & Farner 1966, Dawson et al. 1983, Nolan & Ketterson 1983). Consequently, I converted these data to the number of hours the estimated amount of fat can sustain a specific metabolic rate (Table 1). The metabolic rate I used was $2.5 \times BMR$, which is the estimated rate at the northern boundary of select species' ranges (Root 1988b). The total number of hours this metabolic rate could be sustained was determined at each location by calculating the grams of fat needed per hour to fuel a metabolic rate of $2.5 \times BMR$ ($J^*[bird \cdot h]^{-1}$). Dividing this into the estimated available fat provided the number of hours the amount of fat would sustain that metabolic rate. Night length, which varied by location, was subtracted from this value to obtain the number of hours individuals can survive after dawn without feeding, still assuming a metabolic rate of $2.5 \times BMR$ (Figure 3). In AL where individuals would rarely if ever have to maintain a metabolic rate as high as $2.5 \times BMR$, the available fat at dawn was enough to allow them to survive for an average of 1.0 ± 1.1 hour after dawn without feeding. The average number of hours in TN was shorter than in IN, but not significantly so ($P=0.20$). Consequently, these data were combined resulting in an average of 11.1 ± 1.8 hours. This mean was significantly higher than either AL ($P=0.0001$) and MI ($P=0.02$; Figure 3).

TABLE 1 – Means, standard errors, and sample sizes for various parameters at different locations.

Parameter	MI	IN	TN	AL
Conductance* (n)	2.28±0.07 (3)	2.22±0.07 (7)	2.28±0.08 (9)	2.12±0.08 (9)
BMR+ (n)	64.87±1.86 (5)	60.39±0.70 (2)	59.69±3.22 (2)	56.97±1.13 (4)
Estimate Fat# (n)	3.87±0.55 (8)	4.72±0.67 (9)	4.45±0.26 (9)	2.42±C.18 (13)
Hours++ (n)	4.0±2.1 (7)	12.9±3.9 (9)	9.7±1.2 (11)	1.0±1.1 (13)
Citrate Synthase'' (n)	—	147±10 (4)	146±12 (4)	128±10 (4)
HOAD'' (n)	—	15.9±1.5 (4)	16.1±1.4 (4)	13.4±2.4 (4)

+ in J*(g*h*°C)⁻¹
* in J*(g*h)⁻¹
in g. Text explains the derivation.
++ Number of hours after dawn an individual sustaining a metabolic rate of 2.5xBMR could survive.
'' in micro-moles (g*min)⁻¹

Emzyme Assays

The activities of both CS and HOAD, and the ratio of HOAD to CS were not significantly different among the states (Table 1). They had a grand mean of 140 ± 6 and 15.2 ± 1.0, with ranges of 106 to 178 and 8.6 to 20.0, respectively.

DISCUSSION

A pattern of larger birds extending their ranges farther North into areas with colder ambient temperatures is seen in passerines that winter in North America and that have northern range boundaries associated with particular isotherms (Figure 2). Understanding the mechanisms influencing this pattern will help us understand the commonly found empirical pattern of larger-bodied species generally having larger ranges (e.g. Averill 1933, Van Valen 1973, Reaka 1980, Brown 1981, Brown & Maurer 1989).

Due to colder temperatures and longer nights, Cardinals in the more northerly portions of their ranges must either decrease their heat loss due to conductance, or be able to sustain higher metabolic rates for a longer period of time than do more southerly conspecifics. Comparisons of metabolic responses from four locations indicates that heat loss due to conductance does not vary geographically (Table 1). Therefore, the insulative abilities, i.e. heat loss, of individuals are apparently constant from the southern to the northern extremes of it range.

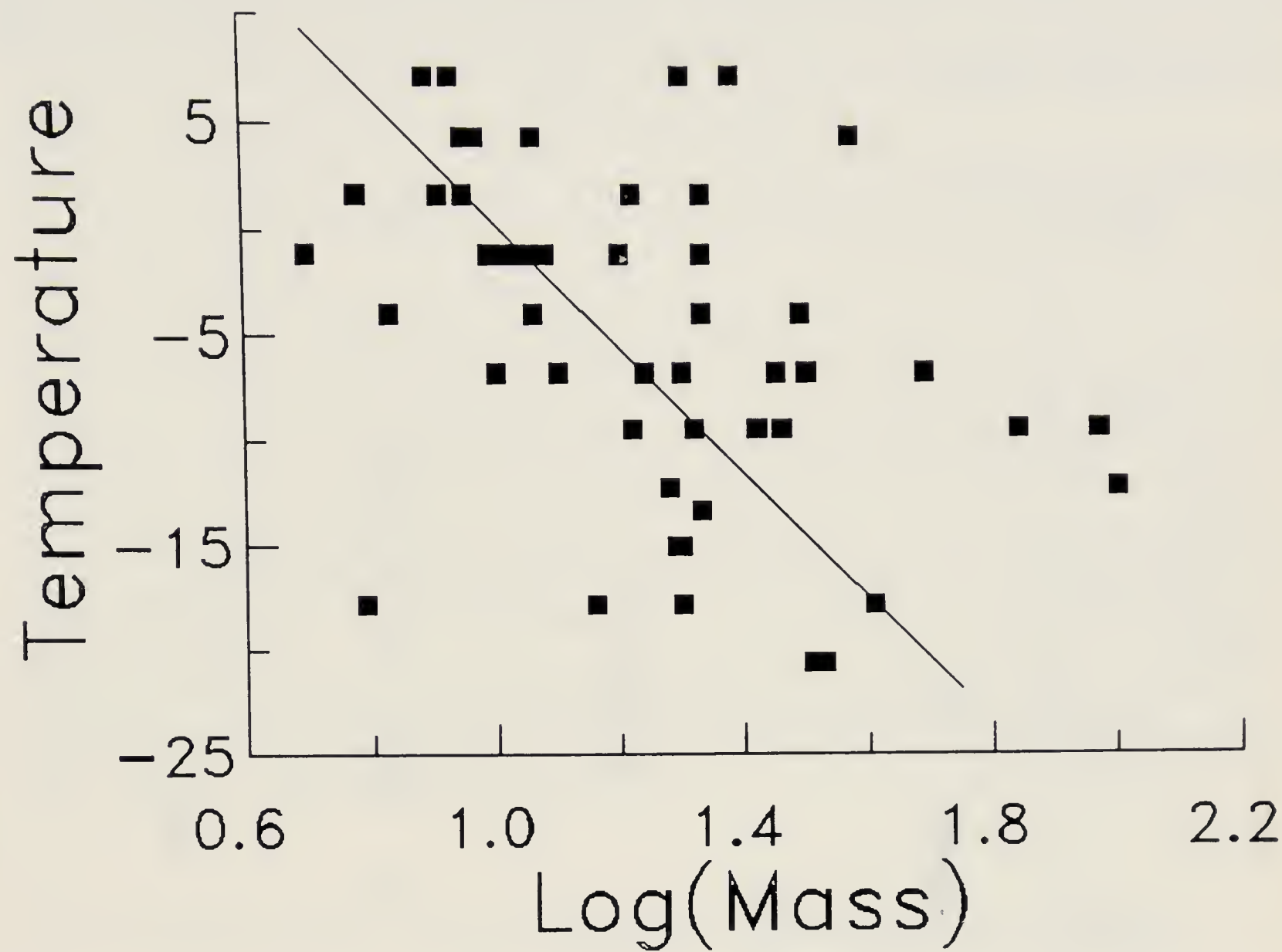


FIGURE 2 - The line defined by $T = 30.5 - 29.68 \log(M)$ (see derivation in "OBSERVED PATTERN" of text) with the values for 50 North American wintering passerines that had northern range boundaries associated with ambient temperature. T is measured in $^{\circ}\text{C}$ and M in g.

Depot fat, which fuels thermogenesis (Carey et al. 1978), could be limited in two ways. First, enough fat cannot be obtained from available food. Second, the enzymes needed to convert the fat to usable energy are not available in sufficient concentrations to facilitate conversion rapidly enough.

The enzyme assays of CS and HOAD provided no indication that enzymes were limited anywhere across their range. The activities of these enzymes per g of muscle did not vary geographically (Table 1).

I have found evidence that the amount of depot fat may indeed be constraining cardinals from extending their ranges farther north. Estimates of the amount of fat available at dusk provides a means of examining energy availability among locations. The meaningful comparison is not of the amount of fat but rather the length of time it can provide sustainable energy for thermogenesis at each of the locations. Night length, ambient temperature and BMR vary with location (Table 1). The number of hours after dawn that a metabolic rate of $2.5 \times \text{BMR}$ can be sustained is significantly shorter for individuals in the North than in the middle portion of the cardinal's range ($M = 4.0 \pm 2.1$, $\text{IN}/\text{TN} = 11.1 \pm 1.8$; $P = 0.02$; Figure 3). Therefore, the amount of depot fat in northern individuals provides very little surplus energy to ensure survival without actively for-

aging throughout most day-light hours. Cardinals in the middle of their range are better buffered against inclement weather, the fuel will maintain thermogenesis longer without feeding. Hence, the amount of depot fat seems to be constraining the range of the Northern Cardinal.

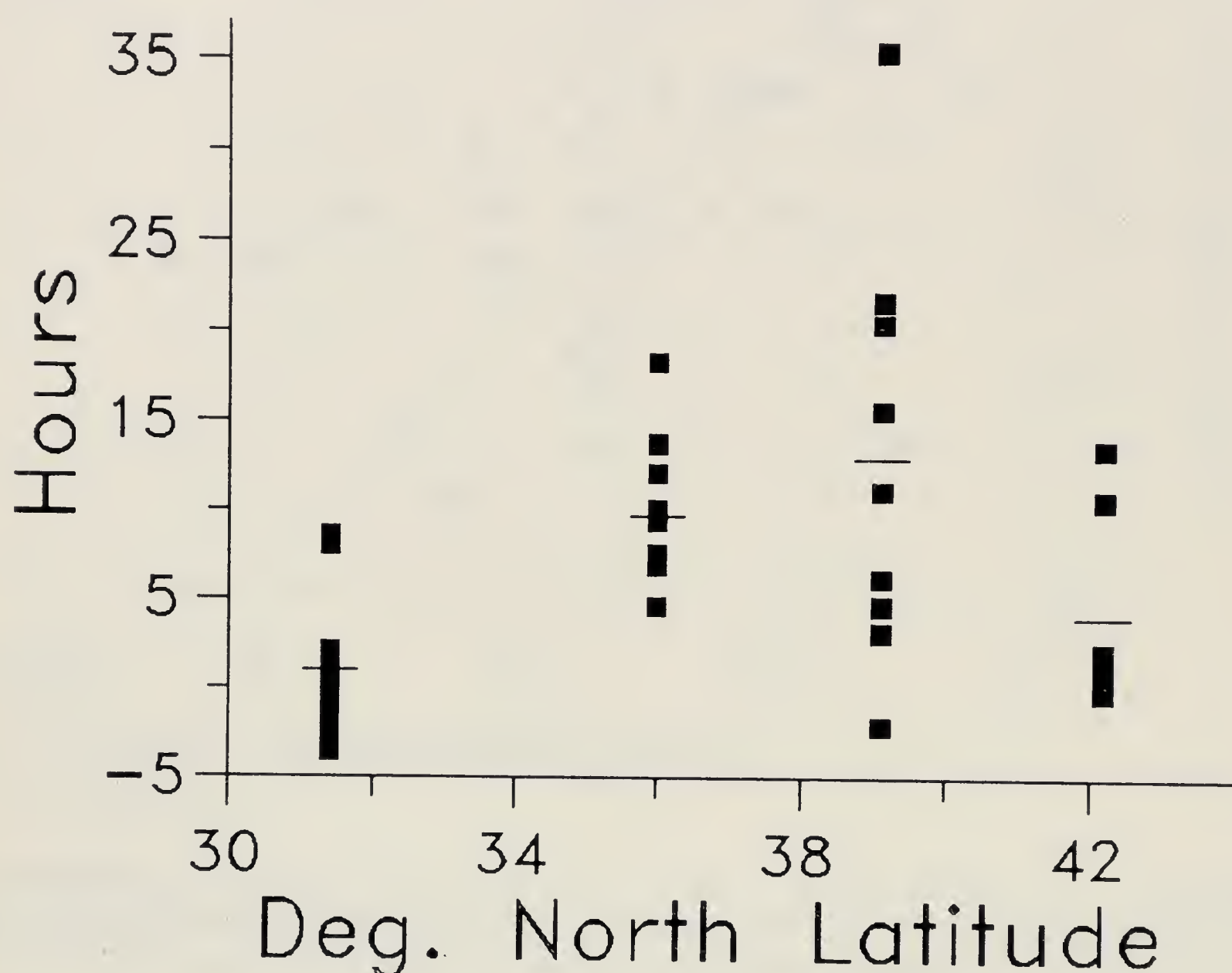


FIGURE 3 - The number of hours past dawn that the average amount of depot fat in Northern Cardinals can sustain a metabolic rate of $2.5 \times \text{BMR}$ in AL, TN, IN, and MI. The average values are indicated with a bar.

Similar studies need to be done on species of different body sizes and range sizes. Finding results similar to the ones in this paper would suggest that homeostatic and environmental variabilities are indeed driving the positive correlation between body size and range size within given taxa. This would be due to the direct relationship between body size and homeostatic variability, this variability and environmental variability, and the latter variability and range size.

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EXTINCTION RATE, BODY SIZE, AND AVIFAUNAL DIVERSITY

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ABSTRACT. Many factors determine the diversity of an avifauna. Although it is not possible to measure all of these factors for all birds in an avifauna, three variables in particular seem to provide a summary of the effects of these many different factors. We examined the statistical distribution of Australian terrestrial birds within a three dimensional space formed by log transformed values of their average abundance, average body mass, and geographic range size. We found that Australian birds had very similar statistical distributions to those documented for North American terrestrial birds. We used data on North American birds to estimate extinction times for various taxa, and found that body size per se was not closely related to estimated extinction time, but that estimated extinction rates were significantly different for four different passerine taxa that differ in their ecological flexibility. We conclude that body size, inasmuch as it affects the complex of adaptations possessed by a taxon, may influence rates of extinction. However, we stress that taxa that show a greater degree of ecological flexibility than other taxa also have lower rates of extinction.

INTRODUCTION

The diversity of an avifauna is determined by many processes occurring on many scales. At one extreme, the success with which individual birds are able to meet their life history requirements determines the stability and rates of change of populations, and hence, the likelihood of extinction for each species. At the other extreme, the history of geological and climatic events on continents through geological time determines patterns of geographical isolation and availability of resources for continental populations, and hence, rates of speciation and extinction. Measuring all of these factors for all species in a continental avifauna is impossible. Hence, we are left with the task of finding a small set of variables that are sufficient to describe the major ecological and evolutionary characteristics that affect the persistence of species if we are to develop an empirically based theory for the maintenance of species diversity.

Three variables seem particularly suitable for this task (Brown & Maurer 1987). As has been discussed in this symposium, body mass is related to a number of factors affecting the ecological properties of species such as metabolic rate, life histories, and foraging behavior. In addition, geographic range size is related to the breadth of ecological conditions that a species can tolerate and average population density is a measure of how successful a species is in turning resources into birds. Hence, examining the statistical distribution of a large number of species in an avifauna among these three variables should provide an indication of the kinds of processes affecting the persistence of species, and hence how species diversity is regulated (Brown & Maurer 1987, 1989).

Each species in an avifauna can be represented by a point in a three dimensional space defined by body mass, average density, and geographic range size (Brown &

Maurer 1987). For any species, if we multiply its values for these variables together, we get the volume of a rectangular box in the space, which is an estimate of the total biomass of the species (Rapoport 1982). The distribution of species of North American terrestrial birds was confined to limited regions of this space (Brown & Maurer 1987). Some of the under-represented combinations of variables were attributed to the higher likelihood of extinction of some species that occupy certain regions of the space (Brown & Maurer 1987). The implication is that certain "strategies" or combinations of density, body mass, and geographic range size are more likely to result in persistence than are others. Species with similar total biomasses may have very different likelihoods of extinction, depending on the particular combinations of the three component variables they possess.

Our purpose in this paper is to compare the distribution of species of Australian landbirds among these variables with the results Brown & Maurer (1987) obtained for North American landbirds. If the avifaunas of these two continents show similar patterns, this would suggest that the processes determining these patterns were similar. Furthermore, we examine the relationship between body size and rate of extinction in North American terrestrial birds in order to examine hypotheses regarding the role of body size variation among species in regulating continental diversity.

METHODS

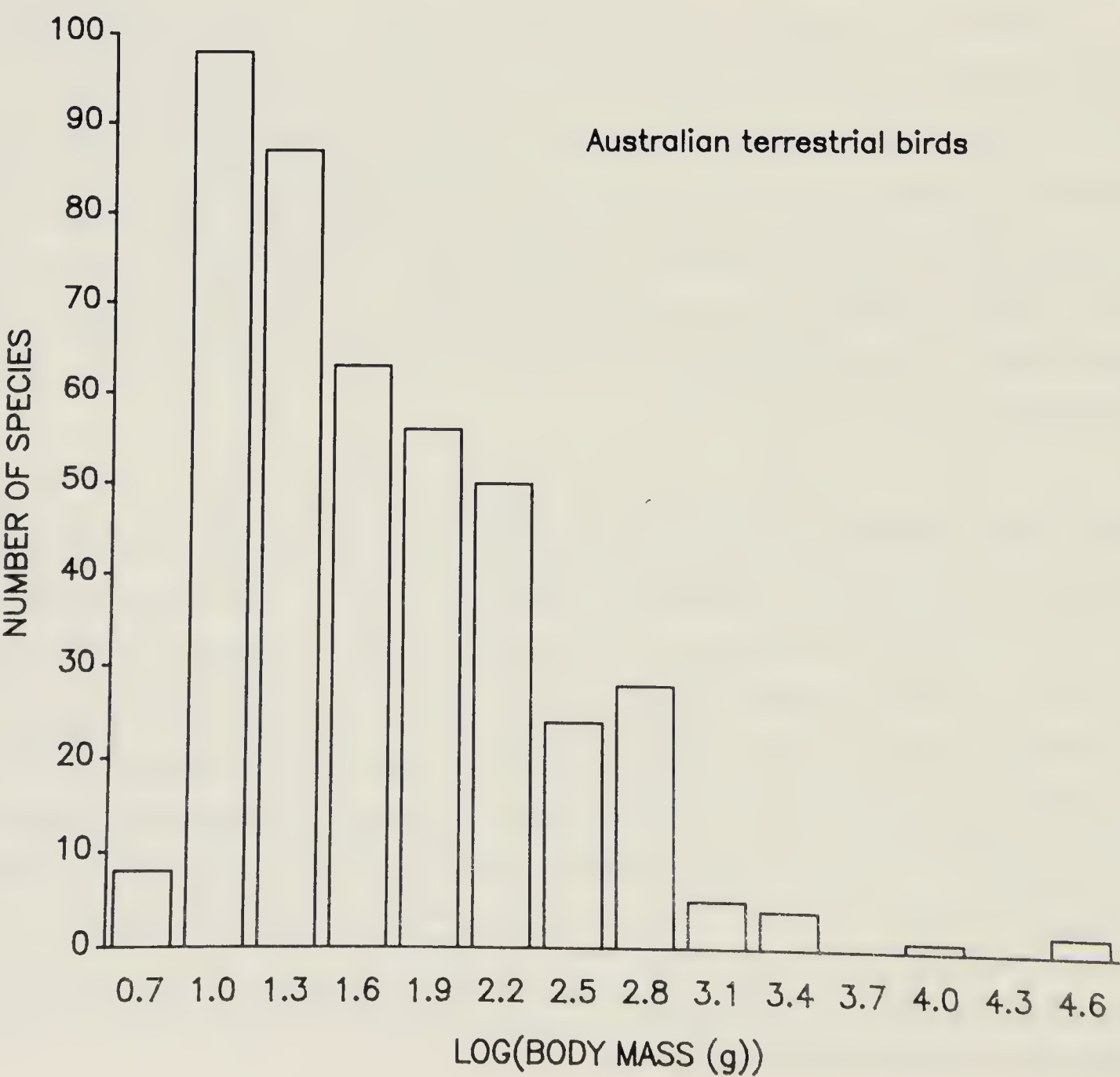
Data on geographic range size of Australian landbirds were taken from Blakers et al. (1984). We used the number of 1 degree latitude-longitude blocks occupied by a species as a measure of the size of its geographic range. A crude measure of average abundance was calculated by dividing the number of records of a species by the number of blocks it occurred in to give an estimate of the average number of records per block occupied (Ford 1990). This measure has many potential shortcomings as a measure of average abundance, which we acknowledge, but there are no published data from comprehensive surveys attempting to estimate abundance for Australian birds comparable to those for North American birds. Therefore, the results obtained using this measure should be considered tentative. Estimates of body masses for most Australian birds were obtained from data collected for the Australian Bird Banding Scheme and from the literature.

To estimate extinction times for North American terrestrial birds, we obtained crude estimates of total population densities as follows. Data from the Breeding Bird Survey (BBS) conducted by the U.S. and Canadian Fish and Wildlife Services (Robbins et al. 1986) were used to calculate the average number of birds counted per BBS route for each of about 350 species. Since a BBS route is composed of 50 stops, and at each stop a circle of radius 0.4 km is censused, a total of about 25 km² are surveyed by each route. Hence, a crude estimate of average density for a species is the average number of individuals seen per BBS route divided by 25 km². This measure of average density was multiplied by the area of a species' geographic range obtained from planimetry of range maps in Robbins et al. (1983) to give an estimate of the total population sizes of birds. There are many sources of potential bias in these data, but like the Australian data, they are the only data that exist to answer the questions pertinent to the present investigation. We view our findings as tentative until better data have been accumulated.

Using estimated total population sizes for the North American birds, we calculated extinction times using Goodman's (1987a,b) model for average extinction time. His model expresses average time to extinction as a function of total population size, the rate of population change (r), and the variance in the rate of population change (V_r). Estimates of r were calculated by obtaining data on clutch sizes for North American birds from C. Harrison (1978) and H. Harrison (1979). Death rates were assumed to average around 50% (Henny 1972, Saether 1989), although this figure is probably too low. Rate of population change was calculated as the difference between birth rate (i.e., clutch size, accounting for multiple broods per year) and death rate. Since these data were measured per year, the resulting extinction times were given in years. The variance in rate of population change was calculated as $V_r = 5r$ using a value intermediate between Belovsky's (1987) extremes of $V_r = 2r$ and $V_r = 7r$. These extinction times must be considered as preliminary estimates because of the crude nature of the data, but they provide an initial indication of how extinction likelihood varies among North American birds.

Extinction rates of four North American passerine taxa were estimated using the following procedure. An extinction curve for each taxa was constructed by plotting extinction time of a species against the number of species with longer extinction times.

FIGURE 1 - Log body mass distribution of 426 species of Australian landbirds.



The tangent of this curve at a given time divided by the number of species at that time is an estimate of the per-species extinction rate. The taxa used were Tyrannidae, Vireonidae, Parulinae, and Icterinae. These taxa represent a range of different ecological strategies from the small-bodied insectivorous parulines and vireonids, to the larger-bodied insectivorous tyrannids, to the even larger, ecologically diverse icterines. Analysis of variance was used to test for significant differences in mean log-transformed per-species extinction rates among the four taxa. Tukey's method for comparison among means (Sokal and Rohlf 1981) was used to test for differences among pairs of taxa.

RESULTS

Distribution of density, body mass, and geographic range size among Australian terrestrial birds

The distribution of body masses for Australian birds was positively skewed on a logarithmic scale (Figure 1). This result is similar to the results that Maurer & Brown (1988) found for North American birds, and Maurer et al. (1991) found for mammals from several continents (see also Brown & Maurer 1989). Ford (1990) plotted log abundance against log geographic range size for Australian terrestrial birds and found a

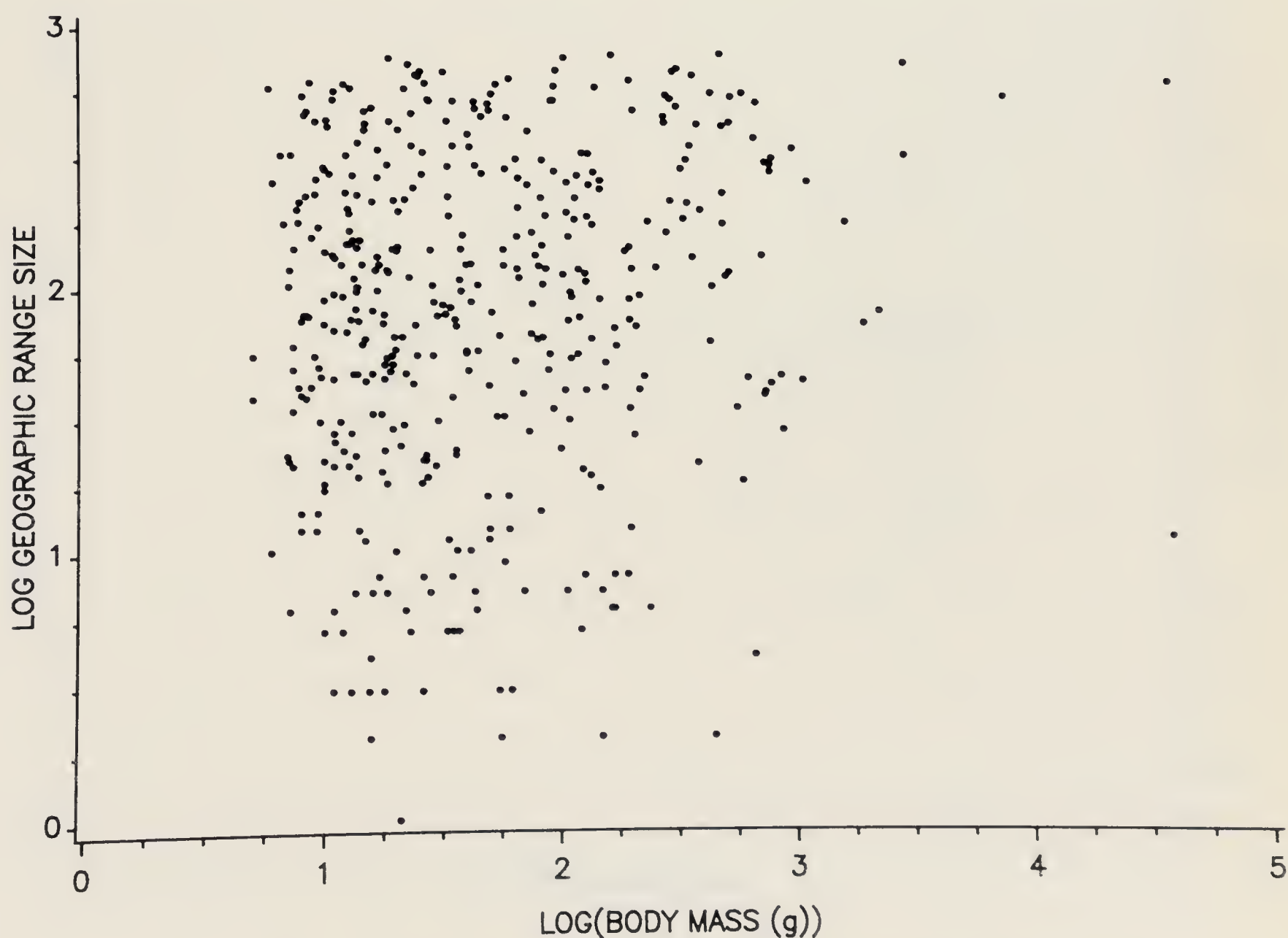


FIGURE 2 - Relationship between log body mass and log geographic range size for Australian landbirds.

pattern similar to that found by Brown and Maurer (1987) for North American terrestrial birds, with relatively few species with small geographic ranges achieving high densities. The distribution of Australian species with log geographic range size and log body mass indicated that the minimum geographic range size increases with increasing body mass (Figure 2). This pattern is nearly identical to Brown & Maurer's (1987) results for North American birds and Brown's (1981) results for North American mammals. The plot of log abundance against log body mass differed in some details to Brown & Maurer's (1987) results for North American birds. Where Brown & Maurer (1987) found that the maximum density of species declined for species both less than and greater than 100g, the Australian data indicated that maximum abundance declined only for species greater than 100g (Figure 3).

Extinction in North American birds

A plot of estimated average extinction times against body mass for North American terrestrial birds indicated that there was no straightforward relationship between body mass and extinction time (Figure 4), although the minimum time to extinction increased with body size above 100g.

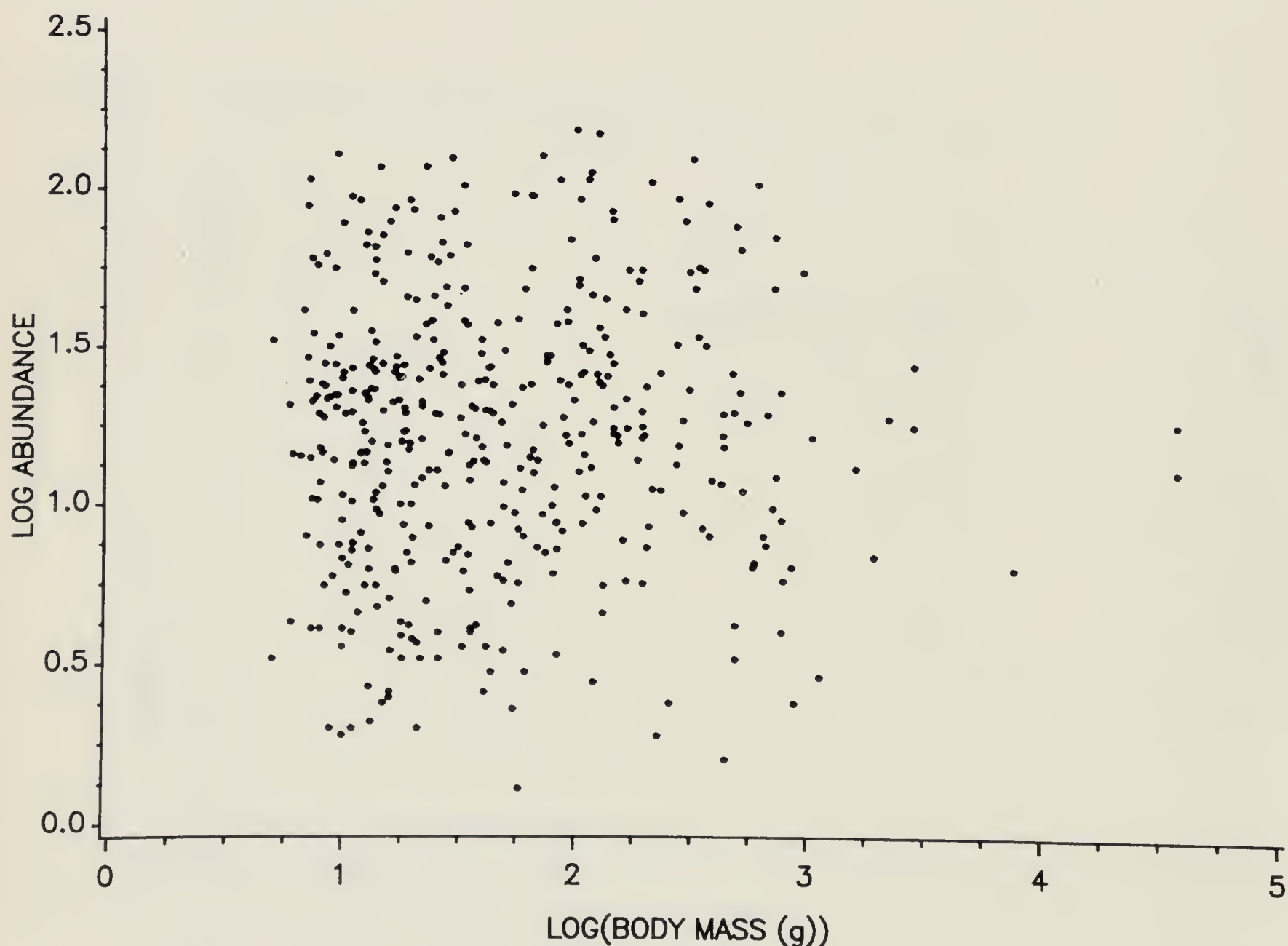


FIGURE 3 - Relationship between log average abundance and log body mass for Australian landbirds.

Extinction curves for four taxa of North American passerines were significantly different (Figure 5). The rate of extinction was clearly greater for the more speciose wood warblers (Parulinae) and flycatchers (Tyrannidae). Of the equally speciose vireos (Vireonidae) and blackbirds (Icterinae), the blackbirds had a lower rate of extinction. Average log-transformed per-species extinction rates were significantly different among the four taxa examined ($F = 4.12$; $df = 3, 83$; $P = 0.009$). The blackbirds had the lowest per-species extinction rates, and the flycatchers and wood warblers had significantly higher rates (Table 1).

TABLE 1 - Average extinction rates of four North American passerine taxa.

Taxon	Number of Species	Average Per-species Extinction Rate ¹ (/1000y)	Standard Deviation
Icterinae	13	0.093 ^a	0.189
Vireonidae	8	0.103 ^{ab}	0.184
Parulinae	43	0.145 ^b	0.265
Tyrannidae	23	0.281 ^b	0.593

¹ Means with the same letter are not significantly different at $P = 0.05$, Tukey's test, after log transforming data.

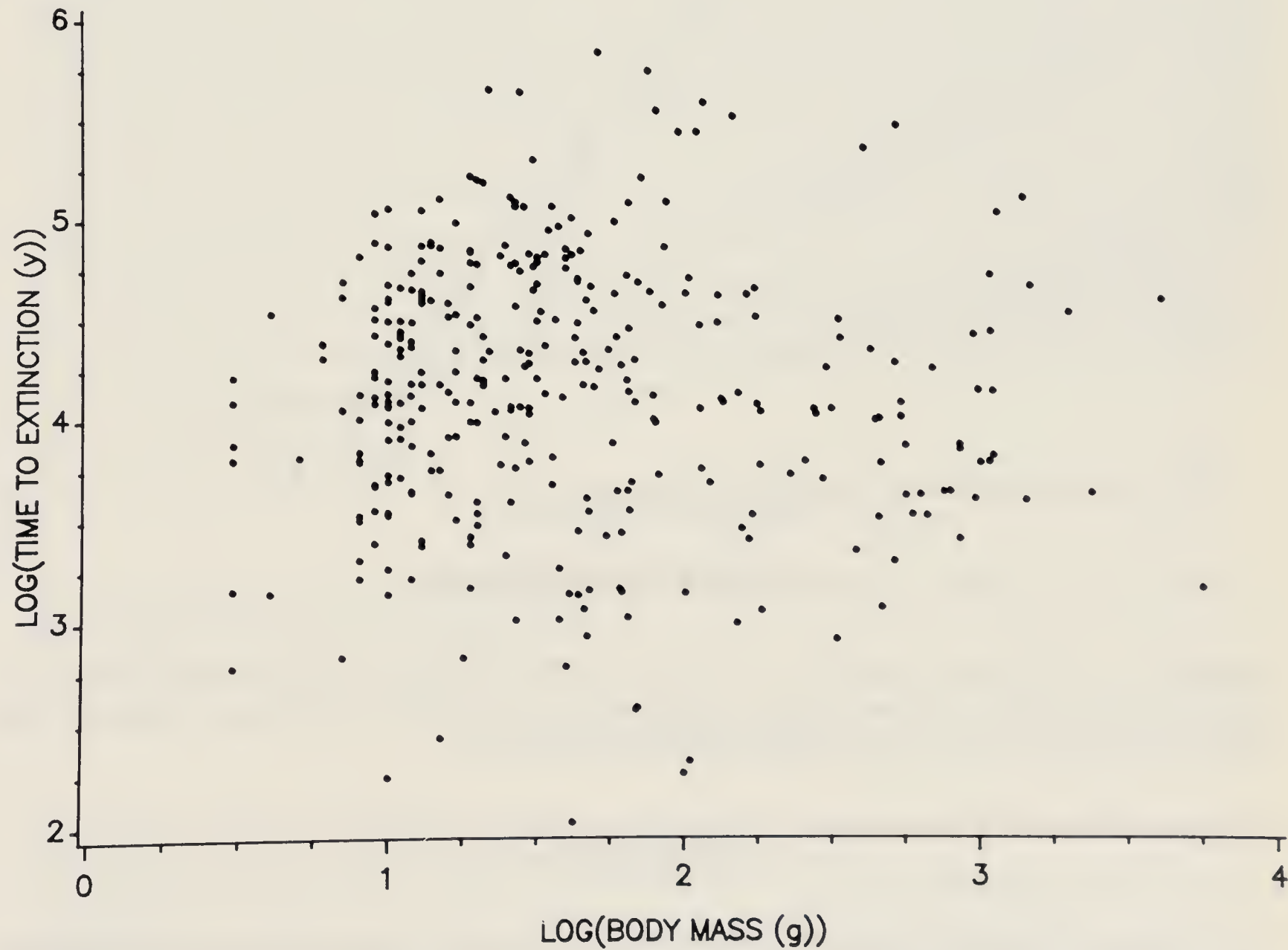


FIGURE 4 - Relationship between log average extinction time and log body mass for North American landbirds.

TABLE 2 - Characteristics of distributions of log body mass among all Australian species of landbirds and those which are considered rare or endangered.

Statistic	All species	Rare and endangered species
Number of species	426	30
Average log body mass	1.67	2.04
Median log body mass	1.55	1.76
Modal log body mass	1.04	1.74
Standard deviation log body mass	0.64	0.64
Interquartile range log body mass	0.93	1.08

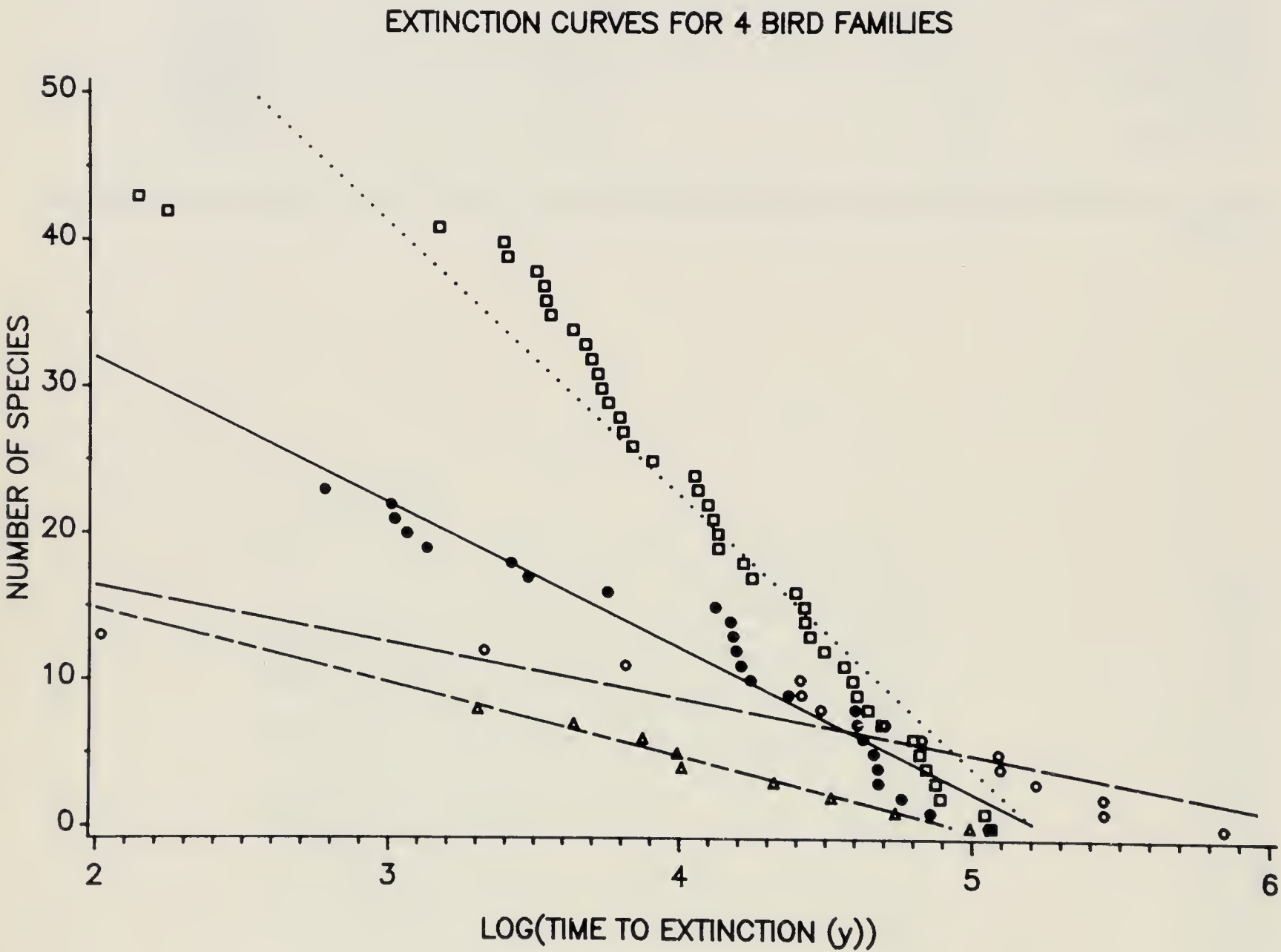


FIGURE 5 - Extinction curves for the North American passerine taxa of wood warblers (squares), flycatchers, (closed circles), blackbirds (open circles) and vireos (triangles). The slopes of the lines are all significantly different ($P < 0.05$).

DISCUSSION

The similar relationships among body mass, geographic range size, and abundance obtained by Brown & Maurer (1987) for North American birds and the present study for Australian birds suggests that the patterns documented here for avifauna are quite general. Similar patterns have been obtained recently by a number of workers examining taxa other than birds (Brown 1981, Strayer 1986, Damuth 1987, Gaston 1988,

Gaston & Lawton 1988, Morse et al. 1988, Maurer et al. 1991). We suggest that whatever processes are ultimately operating to generate these patterns in North American birds, they must also be operating in Australian birds, and other taxa as well. There were some differences between the Australian and North American results, particularly in the distribution of species with log body mass and log average abundance. However, given the different methods of estimating average abundance used for the two avifauna, we hesitate to conjecture whether these differences are due to differences in methods of data analysis or true biological differences between the avifauna.

Brown & Maurer (1987) postulated that the patterns they examined were determined by differential speciation and extinction through geological time. Maurer et al. (1991) further went on to show that the skewed distributions of log body masses seen for many taxa (see also Figure 1) implied that directional selection on body size within lineages was coupled with high rates of extinction in large-bodied taxa and high rates of speciation in small-bodied taxa. Our data for North American birds suggest that extinction likelihood does not increase significantly with body size, but this conclusion must be viewed with caution until better estimates of extinction times are available. Data for Australian birds indicate that the distribution of log body masses among species which are considered rare or endangered is disproportionately made up of species of larger body mass (Table 2).

The most intriguing result we obtained was the finding that different taxa have significantly different rates of extinction. The blackbirds are an ecologically diverse and relatively large-bodied group of passerines. They often maintain relatively high densities when compared with other passerines. Our data suggest that there is a relationship between the tendency of this group of birds to be ecologically diverse and their low rates of extinction when compared to more ecologically specialized taxa. Although body size is one important characteristic of the blackbirds that set them apart from many other passerine taxa, other ecological characteristics they possess also are important in determining their overall diversity. Since each of the groups compared have different evolutionary histories leading to different sets of ecological adaptations, phylogenetic history may be more important in determining the diversity of a group than body size per se.

ACKNOWLEDGEMENT

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CONCLUDING REMARKS: BIRDS, BODY SIZE, AND EVOLUTION

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Studies of birds have provided a great deal of theoretical and empirical information regarding ecology and evolution. Lack's (1947, 1954, 1966) studies exemplify this contribution to biology. Recent interest in the ecological and evolutionary consequences of body size (Peters 1983, Calder 1984) has stimulated a great deal of effort to understand how body size evolves and influences the evolution of other systems of adaptations. It is only natural that studies of the ecological and evolutionary consequences of body size in birds should become an important pursuit of ornithologists.

As has been indicated in this symposium, there are many interesting and important things we have learned from studies of birds and body size. Yet these studies also indicate that there is much more to be learned. The general pattern that seems to emerge from these studies is that body size can explain some of the biology that has the generated patterns observed, but there is sufficient unexplained residual variation after the effects of body mass have been removed to suggest that body size interacts with many other factors to determine the observed ecological characteristics of species.

Probably the most important factor that interacts with body size to influence ecological patterns is phylogeny. Phylogeny is the history of evolutionary relationships among species. Species inherit ecological attributes from their ancestors. Body size is no exception to this rule. Species within higher taxa generally tend to be similar in size and have similar ecological attributes. To make a rough evaluation of the relative roles of body size and phylogeny in determining population densities, I took data on population densities of 380 species of North American birds obtained by Brown & Maurer (1987) and performed a random effects ANOVA (Sokal & Rohlf 1981) to examine the effects of body size and taxonomic status of each species. I divided body sizes into nine classes (see Maurer & Brown 1988) and assigned each species to one of these classes. To evaluate the role of phylogeny, I used the family to which each species belonged as an estimate of phylogenetic relationships among species. Body size class and family were used as random main effects, and I estimated the variance components for each of these effects. The family variance component explained 41% of the total variance in population density, while body size class only explained 1%. Clearly, an explanation for variation in population densities among species must include information on phylogeny. Nagy and Obst's paper in this symposium indicates that residual variation among species in field metabolic rates can be partially explained by phylogeny. In general, to study the evolution of ecological attributes of species, we need better information on phylogenies than we now have for birds. Brooks and McClennan (1990) show how powerful evolutionary explanations become when phylogenetic information is available.

The pursuit of energy by birds is a major factor in determining the ecological success, and hence, fitness of individuals. Body size has a major influence on the rate at which energy is needed (Nagy & Obst) and actually obtained (Goudie & Piatt) by birds. This in turn, influences the ability of individuals to persist in the environment, and more importantly, to use a wider variety of environments (Root). The statistical pattern of individual successes across space determines the size of the geographic range, and Root's intriguing results suggest that body size influences the success of individuals of different species by determining the physiological limitations of individuals to environmental extremes. Root's hypothesized mechanism for limitation by temperature could be extended to any kind of limiting factor.

When species with different geographical ranges are compared, body size emerges as a positive correlate of range size because many of the factors that limit individuals in their response to environmental extremes, such as thermoregulation and foraging rates, are directly tied to the size of the individual. It would be interesting if other correlations between ecological attributes of species, such as population density, can be examined using Root's general approach of searching for factors that limit individuals and asking how the statistical pattern of individual successes is related to body size.

In attempting to catalogue biological diversity, it is evident that we cannot describe the life histories of every species on the planet, indeed, we may not be able to do so even for groups as well known as birds. Carey and Calder's suggestion that body size might provide a way to obtain some estimates of life history requirements of different species may be an important tool for conservation biologists.

The picture developed by the presentations in this symposium suggests that body size is intimately involved in the day to day ecological activities of individuals, and consequently has a significant impact on both individual fitness, and stability of populations. Hence, the evolution of body size might be influenced both by natural selection and by differential speciation and extinction. Natural selection is the consequence of differences in fitness among individuals in a population. If variation in body mass among individuals in populations is heritable (and there is good evidence that it is), then natural selection may operate to change average body sizes within species (Boag & Grant 1981). At the same time, body size influences the rates of life history processes, so that it must also influence the rate of population change. This in turn must ultimately influence the likelihood of extinction of a species. Hence, differential extinction of species of different size may also contribute to the evolution of body size (Brown & Maurer 1986). There is much yet to be learned about the mechanisms involved in generating correlations between body size and ecologically important variables such as metabolic rate, foraging rate, and geographic range size. The answers that we obtain from asking questions about such correlations will tell us much about how evolution occurs. Many of the answers to these questions will come from studies of birds. As we learn more, we will gain new tools to apply to the ever increasing threat of global losses of biodiversity. Such tools cannot be developed without pushing the frontier of knowledge farther than it is today.

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SYMPOSIUM 12

**ECOLOGICAL AND BEHAVIOURAL
ADAPTATIONS OF SOUTHERN HEMISPHERE
WATERFOWL**

Conveners D. F. McKINNEY and M. J. WILLIAMS

SYMPOSIUM 12

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INTRODUCTORY REMARKS: ECOLOGICAL AND BEHAVIOURAL ADAPTATIONS OF SOUTHERN HEMISPHERE WATERFOWL

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In late 1987 the Delta Waterfowl and Wetlands Research Station convened, in Winnipeg, Canada, a week-long symposium on the ecology and management of breeding waterfowl. It was a marvelous talkfeast for swan- goose- and duckophiles from many nations. For me, the highlight was a series of invited review papers which provided superb 'state-of-the-art' summaries of many aspects of waterfowl biology. Their publication is imminent (Batt in press) and they will do much to stimulate and direct studies of waterfowl ecology and behaviour over the next decade.

More recently I have had the opportunity to read a delightful text on waterfowl ecology (Owen & Black 1990), a book that aims to (and indeed will) serve and stimulate the interests of undergraduate and immediate postgraduate students. I suspect it will also prove a useful review document for many long-established waterfowl biologists.

But one conspicuous feature of these compilations, especially when viewed from my home range, is their scant reference to southern hemisphere species and their environments. This is not because Delta's reviewers or Myrfyn Owen and Jeffrey Black have been parochial or less than exhaustive in their literature surveys. It reflects the fact that tropical and southern hemisphere waterfowl are poorly represented in the ornithological literature and have not been the subject of intense or enduring studies like so many of their northern hemisphere counterparts.

This is a pity for it is the tropical and southern hemisphere species that best illustrate and emphasise the diversity and adaptability of the Anatidae.

The ecology of northern hemisphere waterfowl is dominated by the intense seasonality of continental climates. Migration is a dominant feature of their life history. That marked seasonality has impacted upon the evolution of their social systems and breeding strategies and promoted major physiological adaptations.

In contrast, the climates of tropical and southern land masses appear less seasonally extreme and migration is essentially unknown. Nomadism is the response to arid areas but, in general, southern hemisphere waterfowl are sedentary animals. As a consequence social systems are more diverse and breeding seasons are more variable in timing and duration.

In bringing this symposium together, my co-convener Frank McKinney and I have sought to illustrate some of this diversity amongst tropical and southern hemisphere waterfowl. We have chosen specific examples from amongst the ducks (Anatini) and concentrated on the general fields of ecology and behaviour.

Our contributors (and we regret we have none from southern Africa or continental South America) have been asked to highlight behavioural responses to differing ecological conditions. In the process the emphasis has been narrowed down to a consideration of breeding strategies and mating systems.

Arid zone breeding adaptations (Sue Briggs), breeding behaviour of a sedentary tropical resident (Lisa Sorenson), mating system of a river specialist (Clare Veltman), parental care in southern hemisphere *Anas* (Frank McKinney), and ecological and behavioural responses to island life (Murray Williams) is our lineup but they represent just a few of the topics that warranted consideration in this symposium. While all of these contributions will be presenting new and exciting findings, none should be regarded as the last word on their topics. We hope the papers will both inform and, more importantly, stimulate further interest in those waterfowl which live close to or south of the equator.

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BREEDING ADAPTATIONS OF SOUTHERN HEMISPHERE, ARID ZONE DUCKS

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ABSTRACT. Ducks inhabiting the arid zones of the southern hemisphere have similar clutch sizes to other non-sedentary ducks, and longer incubation and fledging times than northern migratory species. Arid zone ducks appear able to use the resource peaks in their environment to produce clutches of equivalent size to most other ducks. However, their incubation and fledging times do not conform with the very brief (< three months) inundation of some wetlands in arid areas, in spite of their ability to breed on temporarily flooded wetlands in arid country.

Keywords: Arid zone, ducks, southern hemisphere, breeding, clutch size.

INTRODUCTION

Arid and semi-arid lands are characterised by low (< 500 mm per year) and variable rainfall (MacLean 1976, West 1983, Evenari 1985). Short, heavy bursts of rain are typically followed by long, dry periods (Nicholls & Wong 1990). These alternating wet and dry conditions produce intermittently flooded, productive wetlands in arid and semi-arid regions, on which large numbers of waterbirds feed and breed (Brand 1966, Frith 1967, Uys & MacLeod 1967, Siegfried 1970, Geldenhuys 1982, Gentilli & Bekle 1983, Maher & Carpenter 1984, Maher 1988).

The specific aims of this review are to determine how clutch sizes, and incubation and fledging times differ between ducks that breed in arid (including semi-arid) regions, and those that breed in non-arid (humid plus sub-humid) regions. It is based on a longer paper which will be published elsewhere (Briggs ms.). The species covered in this review are those in the tribes Anatini and Aythyini (subfamily Anatinae) and in the monospecific genera *Stictonetta* and *Malacorhynchus* (Livezey 1986).

Common and scientific names follow Johnsgard (1978), except where superceded by Marchant & Higgins (1990).

METHODS

Ducks were grouped in six categories (Briggs ms.) by the climate of their breeding habitat (arid/semi-arid or humid/sub-humid), their movement patterns (non-arid taxa only), and whether their mid-breeding latitude is in the northern or southern hemisphere. The categories were thus: arid, southern hemisphere ducks (AS); arid, northern hemisphere ducks (AN); non-arid, partial migrants of the southern hemisphere (PS); non-arid, regular migrants of the northern hemisphere (RN); non-arid, seden-

tary , southern hemisphere ducks (SS); and non-arid, sedentary, northern hemisphere ducks (SN) (Appendix). Waterfowl in the AS and AN categories that mostly or always breed in arid or semi-arid environments (highly arid ducks) were further divided from waterfowl that only sometimes breed in arid or semi-arid environments (partly arid ducks) (Appendix). Clutch sizes, and incubation and fledging times of ducks in these categories were compared.

Throughout this paper, arid includes both arid and semiarid, humid or non-arid includes both humid and subhumid, and ducks and waterfowl refer specifically to the species and sub-species in Appendix. Masses of eggs and female ducks were obtained from Rohwer (1988). The source data and references are available from the senior author. Statistical tests follow Zar (1984). All means are expressed with \pm SE.

RESULTS AND DISCUSSION

Clutch characteristics

The mean clutch size of AS ducks is similar to the mean clutch size of RN and PS migrants, and to that of SN ducks (Figure 1). However, the average clutch sizes of waterfowl in all these groups are significantly larger than the average clutch size of SS waterfowl (ANOVA, $F = 5.64$, $df = 5, 68$, Tukey test, $q = 6.50$, $P < 0.001$) (Figure 1). Clutch sizes did not differ between highly arid waterfowl, partly arid southern, and partly arid northern waterfowl (ANOVA, $F = 1.32$, $df = 2, 19$, $P > 0.25$). The mean clutch size (both hemispheres combined) of sedentary island ducks is 6.7 ± 0.7 ($n=10$), and that of sedentary mainland ducks is 7.7 ± 0.5 ($n=15$).

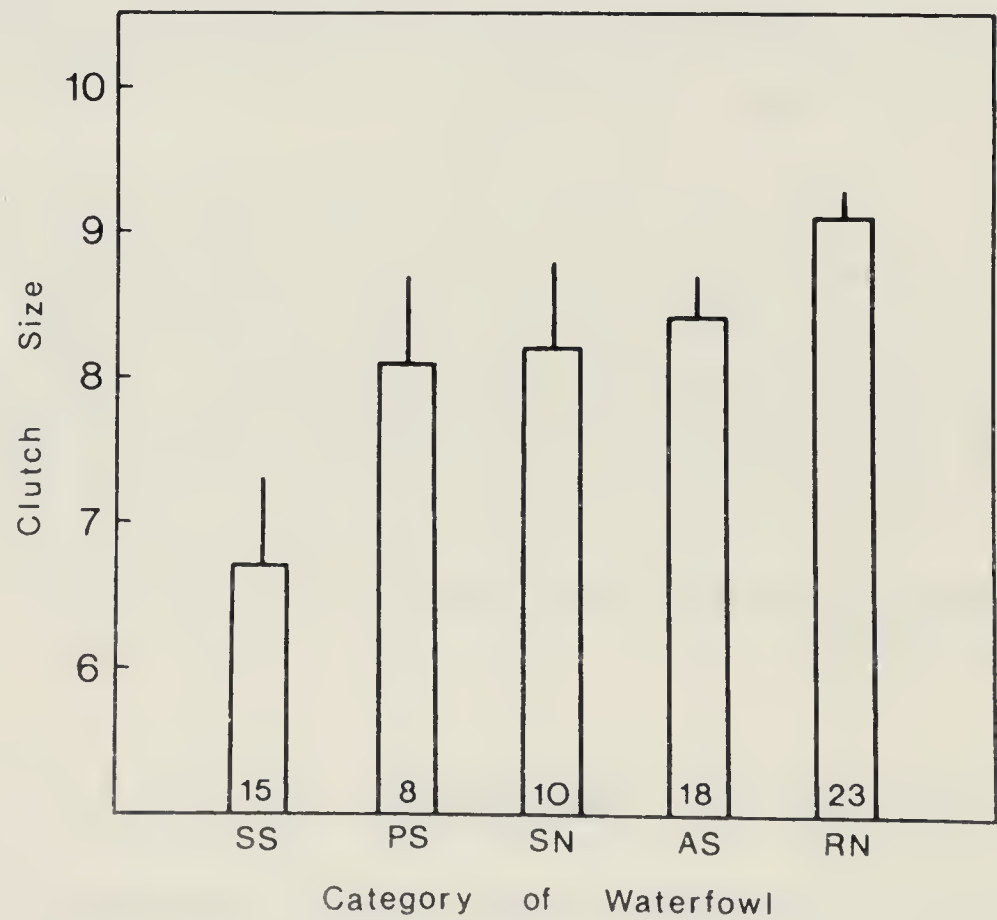


FIGURE 1 - Mean clutch sizes of non-arid sedentary, southern (SS); non-arid partial migratory, southern (PS); non-arid sedentary, northern (SN); arid, southern (AS); and regular migratory, northern (RN) ducks. Vertical bars are standard errors; numbers in the histograms are sample sizes. Data from Briggs (ms.).

The average ratios of egg to female mass (Rohwer 1988) in all categories of ducks, except island forms, are similar (arid (AS plus AN) 0.075 ± 0.003 , $n=20$; regular migrants (RN), 0.072 ± 0.002 , $n=22$; partial migrants (PS), 0.076 ± 0.005 , $n = 8$; sedentary mainland ducks (combined northern and southern hemisphere taxa), 0.077 ± 0.007 , $n=11$). In sedentary island ducks (combined hemispheres) the ratio of egg to female mass is 0.093 ± 0.006 ($n=7$).

Their similar average clutch sizes, and egg to female body mass ratios, indicate that egg production in arid zone ducks is not more constrained by low food resources (or by other environmental factors) before or during laying, than it is in PS or RN ducks. Soils in arid and semi-arid regions generally contain fewer nutrients than soils in humid areas, although there is considerable variation between continents (West 1981, Stafford Smith & Morton 1990). However, even wetlands in infertile arid country may be as high in nutrients as wetlands in more fertile, wetter regions (Williams et al. 1970, Briggs et al. 1985, unpubl. data). This is because run-off water carries nutrients into temporarily flooded run-on areas (Stafford Smith & Morton 1990) which form wetlands, and because wetting and drying of soils, and associated plant growth, enhance cycling of nutrients and organic matter (West 1981, Briggs et al. 1985, references therein). This alternating flooding and drying of wetlands in arid areas enhances production of waterfowl food resources, particularly invertebrates, which allow waterfowl to breed (Frith 1959, Brand 1966, Braithwaite & Frith 1969, Maher & Carpenter 1984). Food supplies for waterfowl increase in wetlands in both arid and non-arid regions following watering after a dry period (Swanson & Meyer 1977, Van der Valk & Davis 1978, Danell & Sjöberg 1982). However, the effects of wetting and drying on productivity of waterfowl foods may be more marked in wetlands in arid regions because the greater variation in rainfall (Nicholls & Wong 1990) increases the area of wetlands that dry and reflood in such regions.

Breeding in arid zone waterfowl, especially in AS ducks, is related to a combination of wetland flooding and photoperiod, with the effect of the former usually predominating (Siegfried 1965, Braithwaite & Frith 1969, Braithwaite 1976 a,b, Halse & Jaensch 1989, Lawler & Briggs 1991). In highly arid ducks, notably in Pink-eared Duck *Malacorhynchus membranaceus*, Cape Teal *Anas capensis* and Grey Teal *Anas gracilis*, laying is entirely dependent on good rains and wetland flooding (Siegfried 1974, Braithwaite 1976 a,b, MacLean 1985; Halse & Jaensch 1989, Lawler & Briggs 1991). At least in Australia, highly arid ducks rarely breed in years when rainfall is sparse and intermittent wetlands are dry or almost so (Frith 1959, Gentilli & Bekle 1983, Halse & Jaensch 1989, Lawler & Briggs 1991). Clutch sizes of arid zone ducks thus appear to be adapted to the resource peaks of their breeding habitat rather than to its average resource availability.

The smaller clutch sizes of SS ducks compared with non-sedentary ducks supports Ashmole's hypothesis which proposes that avian clutch sizes are related to differences in resource levels between breeding and nonbreeding seasons (Ashmole 1963, Ricklefs 1980). Resource levels in the habitats of non-sedentary waterfowl should vary much more than those in the habitats of sedentary taxa, especially ducks on islands. Island waterfowl have lower clutch sizes than mainland taxa Weller (1980). However, clutch sizes of SN ducks are similar to those of non-sedentary ducks, and larger than those of SS ducks.

Incubation and fledging times

Mean incubation time in AS waterfowl is not significantly different from mean incubation times in PS, SS and SN ducks (Figure 2). However, average incubation times in these four groups of ducks are significantly longer than the average incubation time in RN migrants (ANOVA, $F = 3.64$, $df = 4, 64$, Tukey test, $q = 4.42$, $P < 0.05$) (Figure 2). Incubation times of highly arid, of partly arid southern, and of partly arid northern waterfowl do not differ (ANOVA, $F = 0.97$, $df = 2, 19$, $P > 0.25$). Limited data on fledging times indicate that RN ducks fledge significantly sooner than AS or sedentary ducks (ANOVA, $F = 7.46$, $df = 2, 36$, Tukey test, $q = 6.23$, $P < 0.01$) (Figure 3).

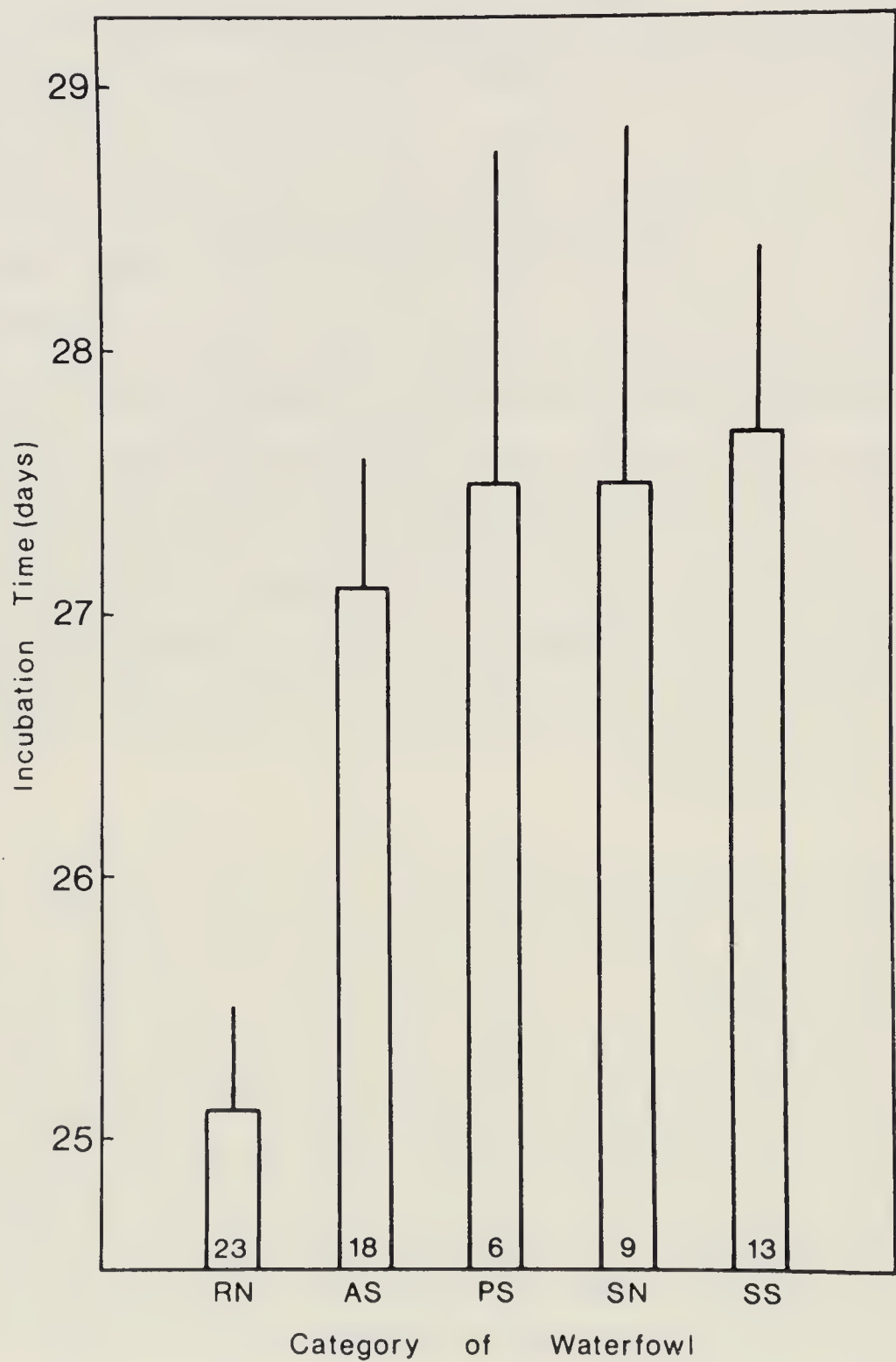


FIGURE 2 - Mean incubation periods of non-arid regular migratory, northern (RN); arid, southern (AS); non-arid partial migratory, southern (PS), sedentary, northern (SN); and sedentary southern (SS) ducks. Vertical bars are standard errors; numbers in the histograms are sample sizes. Data from Briggs (ms.).

Durations of incubation and fledging in waterfowl generally decrease as latitude increases (Lack 1968, Johnsgard 1978). Average incubation and fledging periods in AS and AN species (Figure 2) are as expected for ducks breeding at their latitudes. The relatively long incubation and fledging times in AS and AN ducks, compared with the short times in RN migrants, suggest that wetlands in arid areas are usually inundated long enough for ducklings to hatch and fly (> three months). Not all wetlands in arid

country persist this long, however (Frith 1959, Geldenhuys 1982, Maher 1988), and arid zone waterfowl usually breed on wetlands that hold water for several months, although they may feed on more ephemeral waters (Maher 1988, Lawler & Briggs 1991). Thus, arid zone waterfowl apparently have not reduced their incubation and fledging times to conform with the brief flood periods of some wetlands in deserts and semideserts (also see Fullagar et al. 1988).

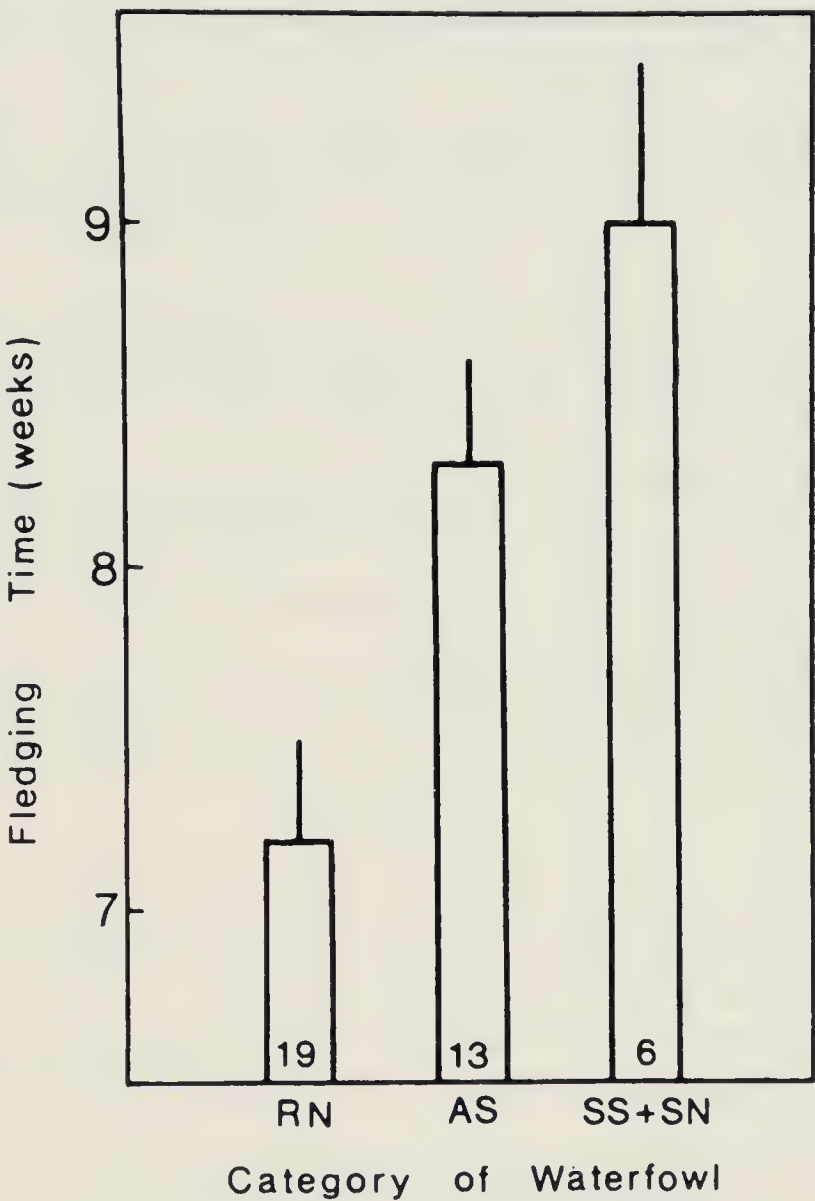


FIGURE 3 - Mean fledging periods of non-arid regular migratory, northern (RN); arid, southern (AS); and combined sedentary, southern (SS) plus sedentary, northern (SN) ducks. Vertical bars are standard errors; numbers in the histograms are sample sizes. Data from Briggs (ms.).

CONCLUSIONS

In summary, arid zone ducks are able to use the fluctuating food resources of their environment to produce clutches of similar size as other non-sedentary ducks. They cope with their variable environment by laying only when conditions are good, not necessarily every year. Arid zone ducks take longer or as long to fledge their ducklings as most other ducks, in spite of their ability to breed on temporarily flooded wetlands.

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APPENDIX

Mid breeding latitudes of arid and semi-arid zone ducks (AS and AN), non-arid regular (RN) and partial (PS) migratory ducks, and sedentary (SS and SN) ducks. The semi-arid and arid zone ducks are split according to whether they mostly (highly arid) or sometimes (partly arid) breed in such environments. The sedentary waterfowl are split into sedentary, mainland (sedentary) and sedentary, island (island) taxa. Data from Briggs (ms.). ¹ Regarded as southern hemisphere breeders.

Taxon	Latitude	Taxon	Latitude
Highly arid			
<i>Stictonetta neavosa</i>	30°S	<i>A. u. undulata</i>	15°S
<i>Malacorhynchus membranaceus</i>	30°S	<i>A. erythrorhyncha</i>	18°S
<i>Anas capensis</i>	12°S	<i>A. smithii</i>	23°S
<i>A. gracilis</i>	30°S	<i>A. rhynchotis</i>	35°S
Partly arid			
<i>A. sibilatrix</i>	45°S	<i>A. platalea</i>	35°S
<i>A. f. flavirostris</i>	40°S	<i>Chenonetta jubata</i>	30°S
<i>A. platyrhynchos diazi</i>	25°N	<i>Marmaronetta angustirostris</i>	37°N
<i>A. castanea</i>	35°S	<i>Netta rufina</i>	33°N
<i>A. superciliosa rogersi</i>	28°S	<i>N. erythrophthalma brunnea</i>	8°S
<i>A. v. versicolor</i>	37°S	<i>Aythya australis</i>	28°S
<i>A. hottentota</i>	17°S	<i>Aythya nyroca</i>	40°N

Taxon	Latitude	Taxon	Latitude
Regular migrants			
<i>Aix sponsa</i>	42°N	<i>A. discors</i>	48°N
<i>A. galericulata</i>	45°N	<i>A. cyamopter septentrionalium</i>	40°N
<i>Anas penelope</i>	58°N	<i>A. clypeata</i>	55°N
<i>A. americana</i>	55°N	<i>Aythya valisineria</i>	58°N
<i>A. falcata</i>	62°N	<i>A. americana</i>	50°N
<i>A. strepera</i>	45°N	<i>A. ferina</i>	45°N
<i>A. formosa</i>	60°N	<i>A. collaris</i>	52°N
<i>A. crecca</i>	56°N	<i>A. baeri</i>	50°N
<i>A. p. platyrhynchos</i>	49°N	<i>A. fuligula</i>	58°N
<i>A. rubripes</i>	47°N	<i>A. marila</i>	62°N
<i>A. a. acuta</i>	58°N	<i>A. affinis</i>	58°N
<i>A. querquedula</i>	51°N		
Partial migrants			
<i>Nettapus pulchellus</i>	15°S	<i>A. s. specularioides</i>	45°S
<i>N. coromandelianus</i> ¹	0°	<i>A. georgica spinicauda</i>	27°S
<i>N. auritus</i> ¹	0°	<i>Callonetta leucophrys</i>	25°S
<i>Anas platyrhynchos maculosa</i>	27°N	<i>Netta peposaca</i>	35°S
<i>A. specularis</i>	46°S		
Sedentary			
<i>Pteronetta hartlaubi</i>	8°N	<i>A. poecilorhyncha</i>	20°N
<i>Cairina moschata</i>	5°S	<i>A. s. superciliosa</i>	45°S
<i>C. scutulata</i>	7°N	<i>A. b. bahamensis</i>	17°N
<i>Anas waigiuenis</i>	5°S	<i>A. versicolor puna</i>	15°S
<i>A. s. sparsa</i>	22°S	<i>Amazonetta brasiliensis</i>	10°S
<i>A. g. gibberifrons</i>	5°S	<i>Rhodonessa caryophyllacea</i>	30°N
<i>A. aucklandica chlorotis</i>	41°S	<i>Aythya novaeseelandiae</i>	41°S
<i>A. playhynchos fulvigula</i>	27°N		
Island			
<i>Anas gibberifrons albogularis</i>	12°N	<i>A. pelewensis</i>	5°S
<i>A. a. aucklandica</i>	50°S	<i>A. luzonica</i>	12°N
<i>A. platyrhynchos wyvilliana</i>	20°N	<i>A. acuta eatoni</i>	52°S
<i>A. p. laysanensis</i>	25°N	<i>A. g. georgica</i>	54°S
<i>A. melleri</i>	20°S	<i>Aythya innotata</i>	20°S

MATING SYSTEMS OF TROPICAL AND SOUTHERN HEMISPHERE DABBLING DUCKS

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ABSTRACT. Many aspects of the behaviour of northern hemisphere dabbling ducks (e.g. seasonal monogamy, female-only parental care) are probably the result of their migratory lifestyle and short, annual breeding season. The sedentary lifestyle and extended or irregular breeding seasons of White-cheeked Pintails *Anas bahamensis bahamensis* in the Bahamas may explain several aspects of this species' mating system that differ from its northern counterparts. During a three year field study, I found that: 1) 4 - 9% of paired males had two mates each year; 2) both long-term pair bonds and mate changes occurred; 3) females alone cared for ducklings but some males continued to escort and defend their mates during brood-rearing; and 4) courtship and competition for mates occurred year-round. A review of the breeding ecology of eight tropical/southern hemisphere *Anas* suggests that variation in movement patterns and in the timing and duration of breeding seasons in these species contributes to greater variation in mating systems and greater intraspecific variability in behaviour.

Keywords: White-cheeked Pintail, *Anas bahamensis*, Anatidae, mating system, polygyny, pair-bond duration, courtship, reproductive strategies, tropics, southern hemisphere.

INTRODUCTION

The mating system of dabbling ducks (*Anas* spp.) breeding in temperate or sub-arctic regions of the northern hemisphere (NH) varies little among species: all have monogamous pair bonds, highly seasonal courtship and pairing, and female-only parental care. Tropical and southern hemisphere (TSH) dabbling ducks appear to show much greater variation in mating systems: pair bonds may persist for more than one year, courtship may occur throughout the year, polygyny has been documented in several species and some species have biparental care. The factors favouring these characteristics are poorly understood, primarily because few TSH species have been studied intensively.

Several recent reviews of mating systems conclude that the basically monogamous mating system of temperate NH ducks is a product of their highly seasonal breeding environment and consequently migratory lifestyle (McKinney 1985, 1986, Rohwer & Anderson 1988, Oring & Saylor in press). New pairs form each year on the wintering grounds and return together to the female's natal area in spring. After escorting and defending their mate during winter and spring, males desert the female during incubation and move to a safe area for the wing-moult. Opportunities for polygyny are limited because 1) males cannot follow more than one female back to the breeding grounds and 2) synchronous breeding and male-biased sex ratios limit the ability of males to acquire a second mate during the breeding season.

Benefits to males of early wing-moult and preparation for fall migration apparently outweigh benefits of remaining with the female and providing parental care and/or

maintaining the pair bond until the next year. Long-term pair bonds, biparental care and polygyny have not been documented in any of these species.

Ecological factors are strikingly different for dabbling ducks breeding in the tropics and southern hemisphere. First, mild climates and variable patterns of rainfall result in more variation in the timing and duration of breeding seasons. In some species, breeding may occur in any month of the year and may continue for many months if suitable wetland conditions persist (Siegfried 1974, Braithwaite 1976a,b, Johnsgard 1978). A second consequence of mild climates is that many TSH species do not undergo long-distance seasonal migrations; some species or populations are sedentary, while others are nomadic (see Briggs, this symposium).

In this paper, I examine the relationship between these basic ecological factors and the variable mating systems of TSH dabbling ducks with emphasis on my own study of the White-cheeked Pintail *Anas bahamensis bahamensis* in the Bahamas. A more detailed analysis of the White-cheeked Pintail mating system is presented in Sorenson (in review).

WHITE-CHEEKED PINTAIL BREEDING SCHEDULES AND MATING SYSTEM

The *bahamensis* subspecies of the White-cheeked Pintail is resident in the West Indies and an adjacent part of South America.

Brackish or salt water ponds and mangrove marshes are the preferred habitat. During a three year field study (1985 - 1987) in the Bahamas, I recorded the breeding activities, social interactions and pair-bond relationships of a color marked population on Paradise Island and other nearby islands and cays northeast of Nassau (Sorenson 1990, in review).

The timing and duration of breeding seasons in this population are variable and greatly influenced by the timing and amount of winter and spring rainfall. The earliest nests were initiated in February in 1987 but not until May in 1985. Breeding seasons also may be extended: nests were initiated over an 86 day interval in 1987. Breeding seasons are even more variable in populations closer to the equator. In Puerto Rico for example, nests have been found in every month of the year (E. Rodriguez, pers. comm.).

Males of breeding pairs in my study population were highly territorial throughout the female's breeding cycle and many males engaged in forced extra-pair copulation attempts. Also, non-breeding was a regular occurrence: an average of 33.6% of females apparently made no attempt to breed each year. These aspects of the White-cheeked Pintail's breeding ecology and social system will be addressed elsewhere (Sorenson, in prep.).

Polygyny

White-cheeked Pintails in the Bahamas usually paired monogamously, but a low level of polygyny (4 - 9 % of paired males) occurred regularly (Table 1). In four of the six trios studied, the male divided his time between two mates, spending more time with one female that was in pre-laying or laying condition and then switching attention to

the second female when the first was incubating and tending her brood. A fifth trio was formed when a male, while still maintaining a pair bond with his first mate who was raising a brood, courted and paired with another brood female whose mate had been killed. In each of these five cases, aggression between the two females was evident whenever the trio was together.

TABLE 1 - Proportion of males pairing polygynously and number of unpaired males for 1985, 1986 and 1987 field seasons (from Sorenson (in review)).

Year	No. paired males which were polygynous (%)*	No. marked unpaired males
1985	1 / 14 (8.3)	9
1986	3 / 34 (8.8)	11
1987	2 / 45 (4.4)	13

* From Sorenson (in review). Data include monogamous pairs and polygynous trios with at least one mate marked.

In the sixth trio, all three individuals associated closely with one another with very little aggression between the females. In this case, the two females bred synchronously, initiating nests within one day of each other. Initially, the male of this trio was simultaneously paired to three females. He copulated with all three females and was engaged in almost constant mate defence as many unpaired males repeatedly tried to approach and court his three mates. After several weeks, one female finally paired with another male. The maintenance of these polygynous pair bonds was remarkable given that the sex ratio of this population was strongly male-biased (1.3 - 1.4 males : 1.0 females) and many males remained unpaired during the breeding season (Table 1). All females were paired and frequently were courted and harassed by both unpaired and paired males.

Two factors probably allow the formation of polygynous bonds in this population. First, because most individuals are sedentary, males have an opportunity to form and maintain pair bonds with two females breeding in the same location. This is not possible for NH dabbling ducks because pair formation occurs away from the breeding grounds. Moreover, individuals are able to interact with one another year-round and year after year, allowing the formation of stable dominance relationships. The fact that individuals “know” each other may facilitate female assessment of male quality. Females that were not protected by their mates from courtship and harassment by other males spent less time feeding and often failed to initiate a nesting attempt. Polygynous males were extremely aggressive, guarded their mates effectively, and were dominant over other males they encountered. Thus, females might pair polygynously with a known male of high quality rather than monogamously with a poor quality male.

Second, extended breeding seasons result in asynchrony in female breeding schedules and may create opportunities for males to acquire more than one mate (McKinney 1985). A male may escort and guard an early breeding female during her pre-laying and laying period and then switch attention to a second female when the first becomes occupied with incubation and brood-rearing. Although this sequence of events occurred in most of the polygynous relationships I documented, the two

females in one trio nested synchronously, indicating that breeding asynchrony was not a prerequisite for polygyny.

Pair-bond Duration

Many pairs remained together for two or more breeding seasons but mate changes were also frequent even when both members of a pair survived to the next season (Sorenson, in review). Of 37 marked pairs studied in 1985 and 1986, both members of 23 pairs were still alive in the following year. Ten of these 23 pairs (43%) remained together in the following breeding season while 13 pairs (57%) divorced. Including data from a brief visit to the study area in 1988, three pairs were known to remain together for three consecutive years.

There are several potential advantages for both male and female birds of remaining with the same mate from year to year. Established pairs may obtain better feeding sites or territories, save time and energy by avoiding courtship, and, through familiarity with patterns of individual behaviour, better coordinate activities and movements (Rowley 1983, McKinney in press). Mate retention is most feasible in non-migratory species (Rowley 1983), and the reunion of mates is more likely in sedentary populations of ducks even when pairs split up during brood-rearing and/or the non-breeding season.

Considering the potential advantages of retaining the same mate, the divorce rate in this population of White-cheeked Pintails seems high. Contrary to results from other studies (e.g. Coulson & Thomas 1983), I found no relationship between breeding success and subsequent mate retention: rates of divorce were similar among pairs that were successful in raising ducklings (7 of 11 pairs) and those that were unsuccessful (6 of 12 pairs, $G = 1.37$, $P > 0.2$).

Courtship and Pairing

Several additional aspects of the White-cheeked Pintail's mating system differ from that of its NH counterparts (Sorenson, in review). First, at least some birds remained paired year-round. Although males did not provide parental care, many males continued to escort and defend their mates for at least part of the brood-rearing period, while other pairs which had separated during brood-rearing reunited after ducklings fledged. Several pairs remained together during the wing-moult, and pairs were also seen during the non-breeding season (September - November).

As in NH dabbling ducks, courtship activity and pair formation occurred well in advance of the breeding season but, in marked contrast to NH species, some social courtship was observed year-round. In particular, males showed intense interest in and actively courted females tending broods. Courtship was also observed in June and July when breeding activity had ended and some birds were beginning the wing-moult. This suggests that the seemingly low level of mate fidelity among successfully breeding pairs in my study may have been a consequence of continuing social courtship and competition for mates throughout the year. It may be very difficult for males and females to keep a good mate from one year to the next.

Siegfried (1974) suggested that if the onset of conditions suitable for breeding is unpredictable, birds may benefit from remaining in pairs year-round so that nesting can begin as soon as conditions permit. Although breeding was seasonal in my study

TABLE 2 - Breeding season, movement pattern, and aspects of the social system of eight tropical and southern hemisphere *Anas*.

Species	Breeding season	Movement pattern	Mating system	Pair-bond duration	Year-round courtship	Biparental care	Male attendance of brood female	Ref. no.
African Black Duck (<i>sparsa</i>) *	seasonal	S	M	long-term	no	no	no	
Cape Teal (<i>capensis</i>) *, **	extended/irregular	N	M & P	long-term?	yes	yes	yes	2, 3, 4
Speckled Teal (<i>flavirostris</i>) **	seasonal/extended	S & M	M & P	?	yes	no?	variable	5, 6, 7
Laysan Teal (<i>laysanensis</i>) *	seasonal	S	M	both long-term & mate switching	no	no	no	8
White-cheeked Pintail (<i>bahamensis</i>) *, **	extended/irregular	S	M & P	both long-term & mate switching	yes	no	variable	9, 10
Silver Teal (<i>versicolor</i>)	seasonal/extended	S & M	M	long-term?	?	yes	yes	7, 11
Chiloe Wigeon (<i>sibilatrix</i>)	seasonal	S & M	M	long-term?	?	yes	yes	11, 12
Grey Teal (<i>gracilis</i>)	extended/irregular	N	M	long-term	?	yes	yes	13, 14

Movement pattern: S = Sedentary, N = Nomadic, M = Migratory. Mating System: M = Monogamy, P = Polygyny. * Field study with marked birds. ** Studied in captivity. Reference numbers: 1. McKinney et al. 1978; 2. Siegfried 1974; 3. Siegfried et al. 1976; 4. Stolen & McKinney 1983; 5. Standen 1976; 6. McKinney 1985; 7. McKinney & Brewer 1989; 8. Moulton & Weller 1984; 9. McKinney & Bruggers 1983; 10. Sorenson 1990, in review; 11. Weller 1968; 12. Brewer 1990; 13. Braithwaite 1976a,b; 14. Marchant & Higgins 1990.

population, the start of the breeding season was quite variable and breeding is more irregular on other islands in the archipelago. This unpredictability probably favours year-round courtship and maintenance of pair bonds in the non-breeding season in White-cheeked Pintails.

Where breeding seasons are extended, female dabbling ducks may be able to raise more than one brood in a single season (Frith 1959, Braithwaite 1976a,b, Fullagar & Davey, in press). Although not documented during my study, one marked female in this population in 1990 (L. Rutan, pers. comm.) successfully fledged her first brood and then initiated a second nest while still paired to the same male (the fate of the second nesting attempt was unknown). Thus, in certain years, the possibility of raising two broods within a 12 month period might favour continued pair-bond maintenance by males during the brood-rearing period. Males also may court brood females to whom they are not already paired in attempts to establish pair bonds with females of proven breeding ability (as evidenced by the presence of ducklings) for a future breeding attempt, either in that season or the next. Both of these male strategies are facilitated by a sedentary lifestyle.

OTHER TROPICAL AND SOUTHERN HEMISPHERE SPECIES

Information is available on the breeding ecology and mating system of seven other TSH dabbling ducks (Table 2). Although intensive field studies of marked birds have been carried out only on the African Black Duck *A. sparsa*, Laysan Teal *A. laysanensis*, and Grey Teal *A. gracilis*, preliminary comparisons with findings on the White-cheeked Pintail are possible.

Polygyny

The White-cheeked Pintail is the only dabbling duck for which polygyny has been recorded regularly in a wild population. Instances of polygyny have been reported in captive Cape Teal *A. capensis* and Speckled Teal *A. flavirostris*, however, and the presence of year-round courtship in both of these species suggests further similarity to the White-cheeked Pintail system. In captivity, the formation of polygynous trios in all three species began with a paired male courting a second female while his first mate was incubating. In each case, the polygynous male succeeded in dominating the second female's mate and breaking up their pair bond. Once paired to the second female, the division of his time between his two mates depended on the stage of their breeding cycles. As suggested for White-cheeked Pintails, the extended and/or irregular breeding seasons of Cape Teal and Speckled Teal may provide opportunities for males to obtain two mates. Factors associated with a sedentary lifestyle also may facilitate polygyny in some populations of Speckled Teal. Cape Teal, on the other hand, are highly nomadic. Siegfried (1974) notes, however, that birds usually travel in pairs and small flocks. If these flocks represent fairly stable groups of individuals, similar factors (e.g. stable dominance relationships) could also apply to this species.

Pair-bond duration

Long-term pair bonds have been documented in African Black Duck, Laysan Teal, Grey Teal and Cape Teal and they are thought to occur in Silver Teal *A. versicolor* and Chiloe Wigeon (*A. sibilatrix*). African Black Duck and Laysan Teal are sedentary, seasonal breeders but neither has biparental care, and pair bonds weaken or break

temporarily during the brood-rearing period (African Black Duck) or incubation (Laysan Teal). The African Black Duck is a highly territorial river specialist: pairs stay together and in residence on the territory almost year-round. Pair bonds can last for several years and only territory holding pairs breed. The importance of cooperation by mates in defense of the territory may favour mate retention in this species (McKinney et al. 1978). Both Cape Teal and Grey Teal have extended and irregular breeding seasons. As in White-cheeked Pintails, it may be advantageous for individuals to remain paired for unpredictable breeding opportunities and for subsequent breeding attempts after the first brood has fledged or is lost (Sorenson, in review).

Grey Teal, Cape Teal, Silver Teal, and Chiloe Wigeon all have biparental care and conspicuously strong pair bonds which apparently remain intact through the wing-moult. In sedentary populations or where pairs remain together during the wing-moult and migration, benefits of desertion for males should be lower as compared to NH dabbling ducks, making both biparental care and the maintenance of long-term pair bonds more likely. Alternatively, biparental care in certain TSH species may enhance duckling survival by improving detection of avian predators (McKinney & Brewer 1989; McKinney, this symposium). Regardless of what factors select for biparental care in TSH species, if it occurs, mate retention may be indirectly affected as well. Strong selection for biparental care would reduce the relative costs of maintaining long-term pair bonds and advantages associated with retaining the same mate may be particularly important in species with biparental care. Selection for either long-term pair bonds or biparental care should indirectly make the other more likely. Biparental care does not occur, however, in all species with long-term pair bonds (e.g. White-cheeked Pintail, African Black Duck, Laysan Teal).

Although the factors influencing mate retention in Laysan Teal are unknown, the annual divorce rate in this species is high (58%, $n = 19$) as in White-cheeked Pintails. Observations of birds in pairs year-round, biparental care and/or male attendance of brood females in many additional species probably contribute to the long-standing belief that pair bonds in TSH dabbling ducks are permanent (Weller 1968, Kear 1970, Siegfried 1974, Johnsgard 1978). Mate-switching has now been found to be common in two of these species. Future studies of individual species need to critically assess whether long-term pair bonds are the rule or simply one variant.

CONCLUSION

Limited and/or nomadic movements, unpredictability in the timing of breeding, and extended breeding seasons all result in a much less ordered annual cycle for TSH dabbling ducks than for their NH counterparts and probably contribute to greater variation in mating systems. Differences in these basic ecological factors probably explain why polygyny, long-term pair bonds, and year-round courtship and pairing occur in White-cheeked Pintails but not in NH dabbling ducks. Other sedentary species (or species in which the sexes travel together) with extended and irregular breeding seasons may share many of the features of the White-cheeked Pintail mating system.

White-cheeked Pintails also show great variability in individual patterns of behaviour. In particular, pair-bond duration and the length of time pairs remain together during the annual cycle is highly variable. Although long-term pair bonds appear to be the

predominant pattern in some species (e.g. Chiloe Wigeon, African Black Duck), it is apparent that not all TSH *Anas* can be characterized as having either long-term or seasonal pair bonds. Similarly, biparental care, male attendance of brood females, year-round courtship, mate-switching, territoriality, and polygyny may occur at varying frequencies in different species or populations. Future study of TSH species, particularly those showing intraspecific variability in behaviour, should greatly enhance our understanding of how ecological pressures shape the social system.

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THE BLUE DUCK MATING SYSTEM - ARE RIVER SPECIALISTS ANY DIFFERENT?

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ABSTRACT. The reproductive behaviour of male and female Blue Ducks *Hymenolaimus malacorhynchos* leads to enduring pair bonds and permanent territories. To evaluate hypotheses about how stability of the river habitat shaped the evolution of this mating system, we measured reproductive success and paternity in a Blue Duck population on the Manganuiateao River, New Zealand. Breeding pairs fledged 1.2 offspring per year, averaged over 23 pairs and 58 breeding attempts. We related reproductive success to pair tenure, and found that pairs of long duration fledged significantly more young than pairs of short duration. Some long-established males therefore exhibited high reproductive success. DNA fingerprinting confirmed the observation that extra-pair copulations did not occur, so cuckoldry was probably nonexistent in this population. Energy requirements were estimated from the basal metabolic rate and represented a very small fraction of the energetic value of the available prey, indicating that Blue Ducks did not defend food resources. Our evidence indicates that male Blue Duck, in common with other waterfowl, defend their mates.

Keywords: Blue Duck, *Hymenolaimus malacorhynchos*, mating system, territoriality, food availability, energetics, evolution, waterfowl.

INTRODUCTION

Worldwide, six species of waterfowl live permanently on rivers. They are the Torrent Duck *Merganetta armata*, Salvadori's Duck *Anas waigiensis*, the African Black Duck *Anas sparsa*, Blue Duck *Hymenolaimus malacorhynchos*, the Bronze-winged Duck *Anas specularis* and the Brazilian Merganser *Mergus octosetaceus* (Johnsgard 1978, Madge & Burn 1988). All six riverine species are distributed in the Southern Hemisphere. In the Northern Hemisphere, Harlequins *Histrionicus histrionicus*, Goosanders *Mergus merganser* and the Chinese Merganser *Mergus squamatus* breed on rivers but migrate to other habitats in autumn.

All of the river specialists studied so far have similar social behaviour. Territories are defended year-round by monogamous adult pairs, and broods are accompanied by the male parent as well as the female except in African Black Duck (Moffett 1970, Kear 1972, 1975, Ball et al. 1978, Williams 1991). Kear (1975) extrapolated from anatomical similarities to suggest that ecological and behavioural adaptations shared by the Southern Hemisphere river ducks originated with a Gondwanaland ancestor, but this phylogenetic hypothesis still lacks supporting biochemical evidence. Brush (1976) was unable to demonstrate shared recent ancestry using feather protein analysis.

Other attempts to understand the evolution of perennial monogamy and territoriality in river ducks have focused on the value of resource defence or mate defence.

McKinney et al. (1978) wrote that exclusive ownership of a stretch of river by African Black Duck pairs evidently served to ensure access to resources like food, nest sites or safe locations for maintenance activities. Such all-purpose territories of ducks in river and shoreline habitats were related to insectivory in particular (McKinney 1985) and the temporal and spatial distribution of food resources in general (McKinney 1986). Oring and Saylor (1989) also related long-term pair-bond behaviour to limited or defendable food resources.

The value of mate defence by male waterfowl was stressed by Gauthier (1988), who argued that the territoriality exhibited by river specialists may represent one end of a continuum from home range behaviour by waterfowl in unstable habitats to enduring site attachment in stable habitats. He reasoned that the expected reproductive success of a drake is made up of two additive components: the productivity of his bonded mate and the offspring resulting from forced extra-pair copulations. In stable habitats where females attempt breeding most years, drakes have most to gain from intense mate guarding behaviour and territoriality. Conversely, males breeding in unstable habitats where nest failure rates may be high could reduce reproductive variance by extra-pair copulations.

Such a causal relationship between habitat stability and behaviour during the breeding season assumes that drakes defend mates rather than food or other resources (Gauthier 1988). This seems a reasonable assumption because overt mate guarding behaviour is widespread in waterfowl (McKinney 1986). A second assumption of the habitat stability hypothesis is that forced copulation is an alternative mating tactic for paired drakes. This has general acceptance (McKinney et al. 1983, Gauthier 1988, Oring & Saylor 1989).

Whether perennial monogamy and territoriality evolved in riverine species because habitat stability promoted mate and site attachment or because habitat stability offered defendable food supplies for breeding pairs and/or their offspring remains to be resolved. Here, we explore the likelihood of food defence using measurements of the use of space, prey availability and metabolic rate in New Zealand's Blue Duck. To our knowledge these are the first quantitative data about food availability obtained from a river duck. We also describe defence behaviour and evaluate Gauthier's two predictions that forced copulations will be rare and the realised reproductive success of drakes will be relatively high with low variance.

METHODS

This appraisal is based on data from a series of completed and ongoing studies of a population of Blue Ducks on the Manganuiateao River in the central North Island of New Zealand. The description of the mating system and measurements of adult survival and productivity were obtained by methods described in Williams (1991). The DNA fingerprinting procedure is reported in Triggs et al. (1991). We refer to earlier analyses of territorial behaviour (Eldridge 1986, Veltman & Williams 1990), diurnal activity (Veltman & Williams 1990) and diet (Kear & Burton 1971), and direct readers to those papers for methodological details.

The rate of metabolism under standard conditions was determined (by BKM McN) from oxygen consumption in two captive-reared adult Blue Ducks maintained in sealed

chambers held at constant temperatures from 10° through 35°C. It was assumed that 20.08 kJ were liberated during consumption of 1 litre of oxygen.

The dry weight of larval Chironomidae per square metre of rock surface was estimated (by MH) in May 1986 and temporal variations in density of Chironomidae were assessed (by KJC) at two-monthly intervals throughout 1989. The two riffles sampled in both studies were the most frequently used foraging area in the territory of the respective resident pairs. Samples for the measurement of dry weight were collected from an area of 123 cm² using a rigid plastic tube with a rubber washer on one end to reduce slippage on the rock surface, and a net on one side. Vertical slits on the upstream side allowed water to flow through and wash invertebrates into the net when rock surfaces were scrubbed. A total of 36 samples was collected in this manner in each of the riffles, from the top, front and sides of submerged rocks. The larvae were later measured, and dry weight was estimated using conversion equations in Smock (1980).

Temporal variations in the number of Chironomidae were determined by removing from each riffle 10 small (0.41-1.33 m²) boulders on each date (5 in July), and scrubbing the larvae from all surfaces into plastic buckets.

Faecal droppings were collected concurrently with invertebrate samples from boulders in 1989 (by LN, IMH and CJV) and Chironomidae were counted in subsamples using mandibles, clypea, and whole heads.

RESULTS

Territorial behaviour and the food supply

Adult pairs of Blue Duck were dispersed at approximately 1 km intervals along the middle section of the Manganuiateao River, and their home ranges were non-overlapping (Williams 1991). Most aggressive interactions between resident adults and their neighbours or newcomers in their area took the form of same-sex challenges. Intruders were usually males, and the male resident responded very aggressively. The bony wing spurs were most pronounced in adult males. Female aggression was mainly directed to juvenile birds of both sexes (Eldridge 1986).

While pairs occupied up to five pool-riffle systems, most of their daily activities were concentrated in only a small part of their range (Veltman & Williams 1990, Williams 1991). Little time in any day was spent in boundary areas. The Blue Ducks vocalised in social contexts and during human disturbance, but did not vocally advertise their residency as do territorial songbirds.

Pairs foraged most frequently in riffles, within a few metres of the bank, and certain riffles were more heavily used (Veltman & Williams 1990). While the remainder of the territory represented potential foraging substrate, the ducks made little use of it. Territory limits did not change markedly from year to year but the number of resident territorial pairs doubled over a ten-year period (Williams 1991). Except for incubation by females, the diurnal time activity budget of territorial pairs prior to and during breeding was dominated by inactivity (Veltman & Williams 1990).

Within these home areas, Blue Ducks caught and consumed a diverse range of aquatic invertebrate larvae, similar to that recorded on other rivers by Kear & Burton (1971). Chironomidae were the most abundant prey in 68 faecal samples, followed by Ephemeroptera. The mean number of chironomid midge larvae per square metre and temporal changes in their relative abundance are shown on Table 1.

Food requirements and prey availability in territories

The mean basal metabolic rate measured from non-moulting Blue Ducks in the thermoneutral zone was 0.790 cm³O₂g⁻¹h⁻¹. Over a 24 hour period, with the basal metabolic rate elevated three times for an active individual, the average energy consumption is 818.64 kJ for a 717g Blue Duck. The prey requirement can therefore be estimated, for invertebrates of known energy value.

Fourth instar *Chironomus zealandicus* larvae generate 17593 + 190J per gram of dry weight (mean of three samples Ryan 1982). This species is found in New Zealand lakes rather than rivers but is similar to the Chironomidae consumed by Blue Ducks on the Manganuiateao River. We do not know the digestibility of these prey, but will assume 50% of their calorific value is assimilated by the ducks. To meet energetic outgoings of about 818 kJ per day eating only chironomid larvae, a Blue Duck must consume approximately 818000/(17593 x 0.5) = 93 g dry weight of prey. The mean estimated dry weight of chironomid larvae in May 1986 was 924 mg per 123 cm² of exposed rock surface. Thus prey were distributed at 75 g m⁻² and a Blue Duck needed to glean less than 2 m² of riverbed per day to meet the total daily energy requirement from this one prey type alone. Chironomid larvae comprised 65-70% of invertebrates on rock surfaces in May 1989 (Table 1).

TABLE 1 – Seasonal variation in mean numbers of larval chironomids per square metre, and in percent abundance of total invertebrates on rocks in two riffles of the Manganuiateao River, 1989.

Month	Territory One Number	Percent	Territory Two Number	Percent
January	375.4	10.6	1955.5	49.0
March	1269.5	22.5	1271.0	23.0
May	9264.7	66.5	10213.3	68.5
July	1486.9	33.5	6780.8	55.7
September	10935.8	87.0	8443.0	75.0
November	390.7	16.0	1677.6	26.8

The mating system

The relationship of paired birds in the Manganuiateao River population was “long-term and constant” (Williams 1991). Females nested between August and December each year, while males stationed themselves nearby throughout the 35-day incubation period. Both adults accompanied the brood, which broke up and dispersed from the natal territory after 70 to 80 days.

Williams (1991) recorded 16 cases of pair formation and an additional 6 instances of two birds acting as a pair to acquire a territory in an undefended area. Three pairs formed after solitary birds had established their occupancy and then attracted a partner and one pair formed when a resident male was challenged and ousted by an

unpaired male. In the remaining 12 cases, pair formation followed death of a partner. Widowed males were seen to displace their male neighbours or bond with formerly unpaired females.

Male Blue Ducks have never been observed to attempt a forced copulation in our study population. The absence of cuckoldry amongst Blue Ducks was supported from DNA fingerprinting analysis which confirmed parentage of 14 offspring (from a total of 10 clutches) of four territorial pairs (Triggs et al. 1991). It seems that an exclusive partnership with a female is the principal route to successful reproduction for male Blue Duck in the Manganuiateao River population.

Survival and productivity

Generally, Blue Ducks are long-lived birds. Males may survive for 7 years or more once they acquire territorial status, but territorial females risk predation while nesting (Williams 1991). Female survival was lower than male survival in five of the nine study years, and overall mean annual survival estimates were 0.91 for males and 0.83 for females. Females may thus have been a limited resource for males.

Of all the nests initiated by Blue Ducks during the study, 54% were successful. On average, 1.2 (SD 1.5) offspring per pair were raised to fledging each year from a mean clutch of 6.0 eggs (Williams 1991). Ten percent of nest failures were followed by renesting (Williams 1991). When productivity is analysed in relation to pair bond duration, significantly more offspring were fledged in each breeding attempt by four pairs with a median pair bond duration of 5 years than by 16 pairs with a median duration of 1 year (Mann-Whitney, $W=751.0$, $P<0.05$). In fact, 69% of 64 fledged young raised in the study area were produced by the four long-established Blue Duck pairs (Figure 1). High reproductive success is therefore an attribute of some males in the Blue Duck population, even if productivity is low overall.

DISCUSSION

Blue Ducks in territories we sampled on the Manganuiateao River did not appear to be defending economic territories, in which defence effort and territory size vary with resource availability. Their foraging activity was limited to a small fraction of the day in a small part of the home range, and prey availability greatly exceeded their caloric requirements by our admittedly crude estimates. Chironomid larvae represented bread-and-butter prey, less preferred than caddis larvae (our unpub. data) and varying temporally in availability, but numerically abundant. A 1 km territory averaging 10 m in width offers up to 10,000 m² of planar foraging substrate, so the ballpark figure of 1.24 m² per adult per day represents a small requirement given the very rapid colonization rates for Chironomidae (Williams & Hynes 1976). Given also that the number of breeding Blue Duck pairs packed into 9.3km of river habitat doubled in ten years, there is little evidence from our results that these Blue Duck defended their food resources.

Rather, we found behaviour consistent with the assumption that Blue Duck males defended their mates. Males engaged in fierce fighting with other males in the presence of females, and such episodes were frequently followed by mate swaps. Males replaced dead partners by breaking the bond of a neighbouring pair, and left the core area of their home ranges if successfully challenged by a newcomer.

Territoriality seemed to isolate breeding pairs, providing a buffer zone and reduced social disturbance of females. Female survival may be lower than male survival, making females a limiting resource for drakes.

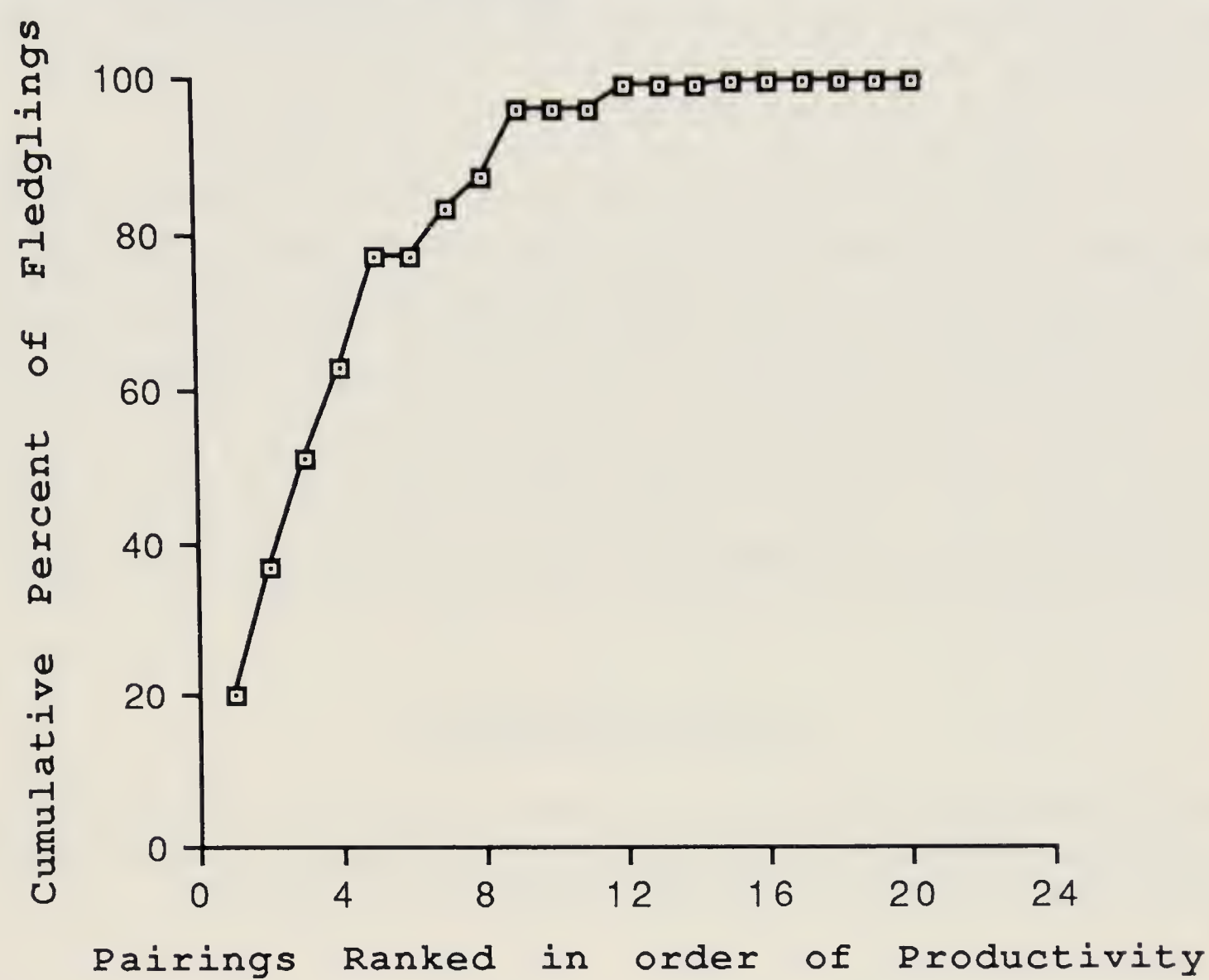


FIGURE 1 – Offspring production from 20 Blue Duck pairings

There was no observational or biochemical evidence of cuckoldry. Thus the realised reproductive success for males depended on breeding with a bonded partner. This is consistent with Gauthier’s (1988) hypothesis, but his prediction of relatively high reproductive success and low variance for territorial males is more problematic. We have found few comparative data on reproductive success in territorial waterfowl. In New Zealand the nesting success of Paradise Shelduck *Tadorna variegata* was 63-68% and breeding pairs fledged an average of 2.6-2.8 ducklings per year (Williams 1979). Similar productivity was measured in Buffleheads *Bucephala albeola* by Gauthier (1989), who found 65% of nests were successful and pairs raised an average of 2.23 offspring. In the latter study a coefficient of variation of about 100% was obtained for reproductive success (G. Gauthier, pers. comm.), compared with 125% for Blue Ducks. In contrast, waterfowl breeding in unstable habitats exhibit very low nesting success. Klett et al. (1988) reported average nest success rates of 6-17% for Mallard *Anas platyrhynchos*, Gadwall *Anas strepera*, Bluewinged Teal *Anas discors*, northern Shoveler *Anas clypeata* and northern Pintail *Anas acuta*, so we expect that offspring production per pair in these species will exhibit extremely high coefficients of variation.

Greatest reproductive output in the Manganuiateao River population was achieved by a few males in long-term pairings, indicating that pair-bond duration or longevity may be important factors in this territorial system.

Predation by introduced mammals accounted for three of 11 known nest failures and probably also explained the disappearance of six incubating females (Williams 1991). Therefore we doubt that we can legitimately estimate the variance in male mating success under natural conditions. Nevertheless, the partners of paired males made a breeding attempt every year and occasionally re-nested after nest failure. Territorial males thus had a high expectation of reproduction in any year.

Based on our results, territoriality in Blue Ducks probably evolved via mate defence as suggested for other waterfowl living in stable habitats (Gauthier 1988). McKinney et al. (1978) found that male African Black Ducks made "heavy and prolonged investment of time and effort in a single female" and Eldridge (1986) described how territoriality was "inextricably tied to pair formation and pair-bond maintenance" in Blue Ducks. Defense of an area larger than required for reproduction and their everyday needs may even be a handicap for drakes, signalling their vigour to potential mates (A. Zahavi, pers. comm.). We do not rule out the possibility that Blue Duck populations experience severe prey shortages following extraordinary floods (P. Ryan, pers. comm.) but our study found no support for the resource defence hypothesis.

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MALE PARENTAL CARE IN SOUTHERN HEMISPHERE DABBLING DUCKS

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ABSTRACT. All northern hemisphere dabbling ducks (Anatini) have female-only parental care. Females brood their ducklings, protect them from predators, and lead them to feeding and resting sites. Males have been recorded with females and broods in many southern hemisphere species, but male parental care (indicated by consistent presence, vigilant guarding, warning, defense, and response to duckling alarm calls) occurs regularly in only nine species. Male presence with broods is variable in another seven southern hemisphere species and may reflect male interest in the female rather than the ducklings. Ecological factors (e.g. hazardous brood habitats) and social factors (e.g. benefits of desertion versus long-term pair-bonding) appear to influence male brood-attendance patterns in this group. Field studies with a focus on intra-specific variation in male behaviour are needed.

Keywords: Southern hemisphere, dabbling ducks, Anatini, *Anas*, parental care, mate-guarding, predation, pair-bond, moult, breeding strategies.

INTRODUCTION

The general pattern of parental care roles in the family Anatidae has been known for many years (Delacour & Mayr 1945) and has been reviewed in detail by Kear (1970) and Afton & Paulus (in press). Of the eight major tribes, biparental care of the young is the rule in whistling ducks* (Dendrocygnini), swans and geese (Anserini), and shelducks and sheldgeese (Tadornini), while female-only care is almost universal in stiff-tails (Oxyurini), sea ducks (Mergini), and pochards (Aythyini). The remaining two tribes, the perching ducks (Cairinini) and dabbling ducks (Anatini), are of special interest because they include species showing both biparental and female-only care. The large tribe of dabbling ducks, including 36 species with a world-wide distribution, provides especially good opportunities to identify ecological and social factors that could influence these variable patterns of parental care. Available information for this group is reviewed here in an attempt to develop promising hypotheses and draw attention to research needs.

Three types of parental attendance patterns can be distinguished in dabbling ducks (McKinney 1985, McKinney & Brewer 1989): (a) only the female is present, (b) both male and female are present, (c) male presence is variable. To investigate why males are always present in certain species but not in others, and why male presence is variable in certain species, detailed information is needed on what males are doing while they accompany females with ducklings, what other options males have, and whether males derive fitness benefits from attending broods.

*Footnote: Common and scientific names of waterfowl tribes and species follow Johnsgard (1978).

A major clue to questions about male presence with broods comes from the geographic distribution of these patterns. Of the 36 species of Anatini, 16 have male attendance (regular or variable), and all of these are southern hemisphere species (Table 1). Factors that could promote this phenomenon in the southern hemisphere are the focus of this review.

TABLE 1 – Incidence of male presence with broods and male parental care in tropical and southern hemisphere dabbling ducks (*Anas* species) *.

<i>Anas</i> spp	Male care usual	Male presence variable	Male usually absent	Male behaviour unknown
<i>waigiuensis</i>	X			
<i>sparsa</i>			X	
<i>sibilatrix</i>	X			
<i>flavirostris</i>		X		
<i>capensis</i>	X			
<i>bernieri</i>		X		
<i>gibberifrons</i>	X			
<i>castanea</i>	X			
<i>aucklandica</i>	X			
<i>melleri</i>			X	
<i>undulata</i>			X	
<i>poecilorhyncha</i>			X	
<i>luzonica</i>				X
<i>specularis</i>	X			
<i>specularioides</i>	X			
<i>georgica</i>		X		
<i>bahamensis</i>		X		
<i>erythrorhyncha</i>		X		
<i>versicolor</i>	X			
<i>hottentota</i>		X		
<i>cyanoptera</i>				X
<i>platalea</i>		X		
<i>smithii</i>		X		
<i>rhynchotis</i>			X	

* Based on McKinney 1985, more recent information in references cited in text, and unpublished data.

BEHAVIOUR OF MALES WITH BROODS

Observations on the nine species of *Anas* in which males are normally present with females and broods (Table 1) have revealed several kinds of male brood-care behaviour (Norman & McKinney 1987, Buitron & Nuechterlein 1989, McKinney & Brewer 1989, Brewer 1990, Marchant & Higgins 1990). Most conspicuously, males spend much time in alert, vigilant postures while the ducklings are feeding and moving about. They also escort isolated ducklings, respond to duckling alarm calls, and behave aggressively toward other water birds near the brood. In response to predators, males have been recorded giving alarm calls and distraction displays, and they may even attack the predators. In exceptional circumstances, if the female is absent, males of several species have been reported raising the ducklings alone. The usual pattern is

for male and female to collaborate closely in these species with biparental care. Females play the major role in maintaining vocal communication with the ducklings, brooding them when they are small, and leading them to feeding and resting sites. In one study of Chestnut Teal *A. castanea*, broods attended by both parents were larger than those accompanied by a single parent (Norman & McKinney 1987). This suggests that duckling survival may be enhanced when two parents are present, but removal experiments are needed to demonstrate this convincingly.

In contrast to these biparental species, the behaviour of males in seven *Anas* species with variable male attendance (Table I) is often more difficult to interpret. In these species, when the male is present with the brood he is usually more interested in the female than the ducklings, but there may be specific differences (see below).

FACTORS FAVOURING DESERTION BY THE MALE

Migratory northern hemisphere *Anas*

In these species, pair bonds typically break during the incubation phase, when the male deserts his mate and leaves the breeding area (Bellrose 1976, Cramp & Simmons 1977, McKinney 1986). Many of these males are known to move considerable distances to reach traditional moulting places (usually large marshes) where they spend the flightless period during wingmoult. Three potential advantages for males have been suggested: (a) the moulting sites enhance individual survival by providing rich food supplies and better escape cover than the breeding grounds; (b) desertion at an early stage in the breeding season allows males to advance through the post-breeding moult, regain nuptial plumage, and build up energy reserves for fall migration, winter courtship, and competition for mates; (c) departure of the male reduces competition for food for the female and brood. Although direct tests of these three hypotheses are difficult, indirect evidence tends to provide support only for the first two.

When females lose their initial clutches to predators, many make renesting attempts, and the same pair bond often persists through the laying of these clutches. In some species, "pairs" have been seen on the breeding grounds late in the breeding season, and it is speculated that these may be failed nesters. Generally this is an uncommon phenomenon.

Southern hemisphere *Anas*

A similar pattern of male desertion appears to be usual in at least some populations of certain southern hemisphere species (e.g. Red Shoveler *A. platalea*, Australasian Shoveler *A. rhynchosotis*) in which males leave the breeding areas and move to traditional moulting lakes (Fjeldsa & Krabbe 1986, M. Williams, pers. comm.). The timing of desertion may vary, however, and in Cape Shoveler *A. smithii* some males apparently remain with their mates until early in the brood-rearing phase (Siegfried 1974). In these species the advantages of desertion to males may be the same as in northern hemisphere migratory species. Information on the occurrence of moult migration is lacking for a number of southern hemisphere species.

FACTORS FAVOURING MALE PRESENCE WITH BROOD FEMALES

A male's presence with a brood could be primarily a consequence of pair-bond maintenance, and this seems to be the case in some species with variable male attendance. By preserving his bond with the female, a male can ensure that he will be able to father any subsequent clutches she lays during the same breeding season. Although males of northern hemisphere *Anas* rarely stay with the female after the end of incubation, desertion can occur during incubation or brood-rearing in some tropical and southern hemisphere species (Sorenson this symposium).

Another possibility is that males remain with brood females to maintain bonds for longer than the current breeding season. Various potential advantages of long-term pair bonds have been identified for birds in general (Rowley 1983), and several authors have suggested that these could apply to southern hemisphere waterfowl. Maintenance of pair bonds could save time when conditions favourable for breeding arrive and/or persist in unpredictable habitats (Siegfried 1974). Alternatively, after a successful breeding effort it could be advantageous for the same compatible individuals to remain paired for subsequent breeding attempts, and compatibility of mates should be especially important in species with biparental care.

The presence of an escorting male can be beneficial to females also. In addition to benefits for both partners relating to future breeding attempts (as noted above), male vigilance and guarding can enable females to feed without disruption. This factor is especially relevant for females in the early stages of brood-rearing when they need to recover from the energetic costs of incubation.

FACTORS FAVOURING BIPARENTAL CARE

Little attention has been given to identifying factors that promote male care in certain *Anas* species but not in others. Males activities while escorting ducklings suggest three potential benefits for the young: (a) promoting brood cohesion, (b) providing protection against predators, (c) enhancing duckling feeding efficiency. I propose that characteristics of brood habitats and the predation pressure to which ducklings are exposed may impose a greater need for male assistance in certain species. There is suggestive evidence along these lines for six biparental species.

River habitats

Two *Anas* species, the African Black Duck *A. sparsa* and Salvadori's Duck *A. waigiensis* raise their broods on rivers. The latter species occupies "white water" stretches of mountain streams, similar to the habitats preferred by the Blue Duck *Hymenolaimus malacorhynchos* and Torrent Duck *Merganetta armata*, and biparental care is strongly developed in all three species. These river habitats are especially hazardous for ducklings because of the high risk of being swept away by the current and becoming separated from their parents. Apart from being exposed to greater danger from attack by predators, lack of parental vigilance may adversely affect the growth of isolated ducklings (Williams 1991), presumably by reducing feeding frequency and/or efficiency. Female-only brood care (at least during daylight hours) is characteristic of African Black Ducks in the regions where this species has been observed, but many of these rivers are relatively slow-flowing and perhaps they do not present such extreme hazards for ducklings.

Open habitats

Three biparental species use brood-rearing habitats that are often very open and devoid of escape cover. Cape Teal *A. capensis* use open saline lakes and lagoons in southern and eastern Africa. Crested Ducks *A. specularioides* breed on Patagonian and Andean lakes and seacoasts with rocky shorelines. Chiloe Wigeon *A. sibilatrix* broods use open wetland habitats where they feed on aquatic plants at the surface, often far from shore.

Terrestrial habitats

Waterfowl that feed on land by grazing are especially vulnerable to predators because often there is no escape cover and they cannot use diving as a method of escape. Brewer (1990) has shown that Chiloe Wigeon broods frequently leave the safety of wetlands to come out on land to graze on nearby grasslands where avian predators hunt, and that males can effectively contribute to brood defense by remaining vigilant and giving alarm calls. Similar hazards may be faced by some populations of island dwelling Austral teal (eg. *A. aucklandica*, Williams et al. this symposium) in which males show vigorous defensive behaviour against predators while escorting broods. The importance of biparental care in ducks that specialize in grazing has also been pointed out by Kingsford (1990) in regard to the Australian Wood Duck *Chenonetta jubata*, a member of the perching duck tribe (Cairinini).

Occluded habitats

In addition to the hazards associated with their terrestrial life, *aucklandica* broods characteristically occupy dense vegetation where vision is often impaired and the risk of ducklings becoming lost may be high. Preliminary observations on Silver Teal *A. versicolor* broods indicate that they also prefer to feed in dense emergent vegetation (McKinney & Brewer 1989).

There remain three biparental species for which habitat features that might promote male brood-care have not been identified. These are the Chestnut Teal, Grey Teal *A. gibberifrons*, and Bronze-winged Duck *A. specularis*.

VARIABLE MALE PRESENCE WITH BROODS

The presence of males with females and broods is variable in seven species (Table 1). Field studies on Speckled Teal and Brown Pintail (unmarked birds) indicate that a number of factors probably contribute to these variations (McKinney & Brewer 1989). Male Speckled Teal appear to vary individually in their attendance patterns; some broods consistently have a male present while others have no male present. Similar consistent patterns of male attendance were observed in many Brown Pintail broods, but part-time attendance was shown by some males. Observations on a marked population of White-cheeked Pintails (Sorenson ms in review) revealed great variation in male attendance; some males were consistently present, others were sometimes present, others were absent. In all three species, males show little or no interest in ducklings and, apart from consistent following by some individuals, males show no obvious brood-care behaviour. Attending males do show interest in the brood female, however, and therefore in these species male presence with broods appears to be primarily a consequence of persistence of the pair bond in anticipation of subsequent breeding attempts.

In these species it is often difficult to decide whether an attending male is the female's mate. Sorenson (ms in review) has shown that brood-tending female White-cheeked Pintails are preferentially courted by males (including males that are paired to other brood-tending females) and this can lead to the formation of new pair bonds. Courtship of brood females has been noted also in Red Shoveler (McKinney & Brewer 1989).

COMPETING MALE REPRODUCTIVE OPTIONS

Male dabbling ducks have several reproductive options in addition to seasonal monogamy (McKinney 1985) and the possibility of conflicts with male brood-care should be considered. The combination of seasonal monogamy and forced extra-pair copulation (FEPC) in a mixed reproductive strategy appears to be a common pattern in migratory species of *Anas* with short, regular breeding seasons in high latitudes. In these species the main period for FEPC activity (i.e. while females are fertile) is usually over before broods hatch, and therefore FEPC is not likely to inhibit male brood attendance.

Male breeding options are more varied in tropical and southern hemisphere species with extended and/or irregular breeding seasons. In addition to monogamy+FEPC, males of several species also engage in extra-pair courtship, mate-switching, and polygyny (McKinney 1985, Sorenson 1990). These activities entail investments of time and effort in assessment and securing of alternative or additional mates, and they are likely to conflict with male brood attendance. Little is known about the ways in which males resolve such conflicts, but information from White-cheeked Pintails in the Bahamas is enlightening (Sorenson, ms in review). The occurrence of complex mixed male strategies (including mate-guarding, territory-defense, FEPC, and polygyny), together with a high incidence of non-breeding, evidently produced great individual variation in male behaviour in this population. One consequence was great variation in pair-bond duration; some birds remained paired together over several breeding seasons, while others switched mates. This study provided firm evidence that males may attend broods in order to preserve their pair bonds, and that such behaviour need not entail male parental care. Other males may desert their mates and broods, or associate with them only part of the time while they also spend time courting other breeding females. Similar complex mixed male strategies and variable male presence with broods (without obvious parental care) are present in Speckled Teal (McKinney 1985, McKinney & Brewer 1989, unpublished data).

The extent to which males which do contribute parental care are able to engage also in polygyny is not yet clear. The Cape Teal may be a species in which males can combine these activities, because courtship occurs year-round and polygyny has been recorded in captives (Stolen & McKinney 1983). On the other hand, tendencies to maintain long-term pair bonds appear to be very strong in other biparental species (notably Chiloe Wigeon and Silver Teal), and perhaps polygyny is not an option in these species.

CONCLUSIONS

Male brood-care patterns in dabbling ducks fall into three categories: (a) male deserts and provides no care, (b) male actively contributes to protection of ducklings, (c) male sometimes accompanies female and brood but gives little or no care. Benefits to males of deserting and leaving their mates to care for the ducklings alone appear to be especially important in migratory *Anas* species with short, regular, annual breeding seasons in high latitudes. This is characteristic of most northern hemisphere species. By deserting, males can move to safe sites for the post-breeding wing-moult and they can begin the wing-moult earlier in preparation for the courtship season.

Biparental care occurs in nine southern hemisphere species. Male participation may be favoured in six of these species because they breed in habitats that appear to be hazardous for ducklings. Biparental care and long-term pair-bonding are likely to be closely linked and mutually reinforcing characteristics.

Variable male presence with broods is characteristic of seven tropical/southern hemisphere species and appears to reflect male interest in the female rather than the ducklings. Opportunities for mate-switching and polygyny are probably greater in species with extended and/or irregular breeding seasons, and participation in these activities helps to account for variable male presence with broods. The extent to which male brood-care conflicts with polygyny is not clear.

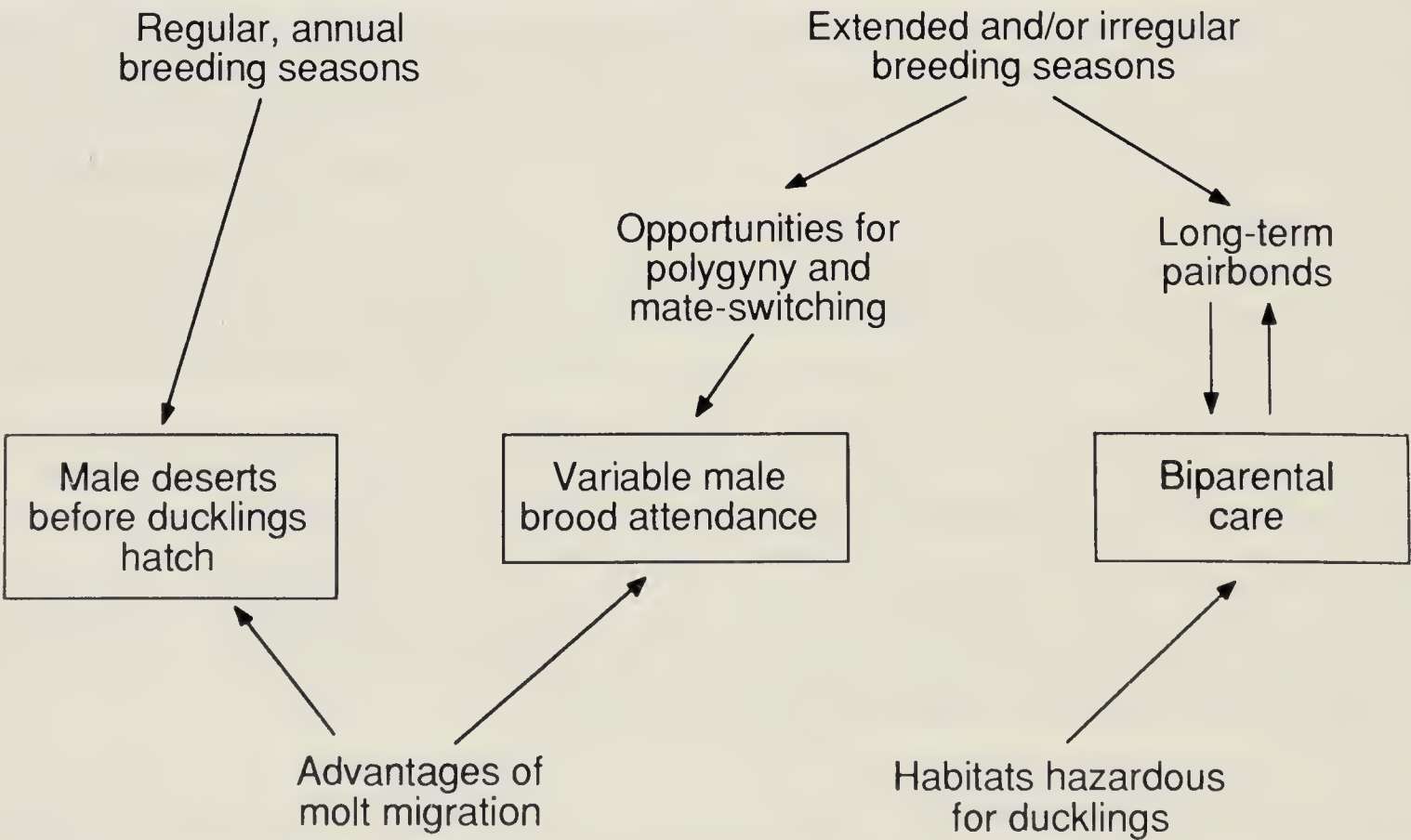


FIGURE 1 – Factors believed to influence the occurrence of male parental care in dabbling ducks.

Highest priority for future research is for long-term studies of marked birds. The presence of males with broods and the roles they may be playing in brood-care is an intriguing topic for research, calling for detailed examination of the overall social system of each species. Especially valuable insights on male options and priorities should come from species showing intrapopulation and intra-specific (eg. racial) variations in male behaviour. More information is needed on the relative vulnerability of ducklings to predators in different habitats. Field experiments (e.g. removals) are needed to test hypotheses on male parental care.

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ECOLOGICAL AND BEHAVIOURAL RESPONSES OF AUSTRAL TEAL TO ISLAND LIFE

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ABSTRACT. Responses of Austral teal to island life were investigated by comparing the morphology, habitats and foods, breeding characteristics, social system, and courtship behaviour of Chestnut Teal *Anas castanea*, New Zealand Brown Teal *A. aucklandica chlorotis*, Auckland Islands Teal *A. a. aucklandica* and Campbell Island Teal *A. a. nesiotis*. By treating them as a sequence from continental (*castanea*) to large island (*chlorotis*) to small island (*aucklandica*, *nesiotis*) forms there was: (i) a reduction in body size and a disproportionate decrease in wing length leading to flightlessness; (ii) a shift from a generally omnivorous to a predominantly carnivorous diet with a concomitant increase in metabolic rate; (iii) increased exploitation of terrestrial habitats and a more cursorial habit; (iv) a reduction in clutch size accompanied by increased egg size, longer laying interval, longer incubation period, a larger hatchling and, in *aucklandica*, faster duckling growth; (v) a change in social organisation from the seasonally social and dispersive to year-round territoriality; (vi) an increase in aggression; and (vii) loss of conspicuous attention-seeking displays (Head-up-tail-up, Down-up) and those occurring in long display sequences and greater use of more subtle displays derived from comfort movements.

Keywords: Austral teal, Chestnut Teal, Brown Teal, Auckland Island Teal, Campbell Island Teal, *Anas castanea*, *Anas aucklandica*, morphology, ecology, behaviour, insularity.

INTRODUCTION

David Lack (1970) and Milton Weller (1980) both appraised the ecological characteristics of waterfowl (Anatidae) inhabiting small oceanic islands. They noted the tendency for small islands to have but one species present, for that species to be derived from a nearby extant continental form (usually *Anas*) with a tolerance of estuarine or marine habitats, for the island form to be smaller and with different body proportions to those of its presumed ancestor, and for it to occupy a wider ecological niche. Both authors noted the tendency for island forms to have shifted from an r- to a K-selected reproductive strategy (by reduction of clutch size and increase of egg size) and from dichromatic to monochromatic plumages.

In this paper we give substance to some of these generalisations as they apply to some of Delacour's (1956) "Austral teal" and we extend the analysis to consider some behavioural changes that appear to be consequences of the island lifestyle.

The Austral teal we consider are the Australasian inhabitants comprising the pan-continental and nomadic Grey Teal *Anas gibberifrons** of Australia, New Zealand and

* Nomenclature follows Kinsky (1970).

New Guinea (but ranging as far south as Macquarie Island and north to the Solomons), the Chestnut Teal *A. castanea* of southwest and southeast Australia and Tasmania, the Brown Teal *A. aucklandica chlorotis*, once widespread on New Zealand's three main islands and Chatham Islands, and two flightless sub-Antarctic forms restricted to the Auckland Islands *A. a. aucklandica* and Campbell Island *A. aucklandica nesiotis*. However, in this presentation most of our comparisons involve only the four brown-plumaged forms, *castanea*, *chlorotis*, *aucklandica* and *nesiotis*.

Austral teal appear to be very closely related (Livezey 1990). Charles Daugherty (in prep., pers. comm.), using gel-electrophoresis of blood proteins, determined that *castanea* and *chlorotis* were separated at a genetic distance most commonly associated with infra-specific variation in birds (Nei 1978, Barrowclough & Corbin 1978) but *chlorotis* and the sub-Antarctic teal were further apart; *chlorotis* and *aucklandica* could be distinguished at one of the 14 loci examined and, although *chlorotis* and *nesiotis* also differed at one locus, this was different from that which separated *chlorotis* and *aucklandica*. Given that all 54 *chlorotis* examined were homogeneous at all loci, and *castanea* were polymorphic at only one, these results suggest that the sub-Antarctic teal are the result of two quite independent colonisations at different times and, perhaps, from different sources and that flightlessness has evolved independently in both sub-Antarctic forms. This may imply that the sub-Antarctic teal are descended from continental, not New Zealand stock and that *chlorotis* is the most recent colonist of the New Zealand region.

RESULTS

Morphometrics

Livezey (1990) has compared the morphology of the Austral teal from museum study skins and skeletal material. Our field measurements of live birds confirm his findings and show (Figure 1): (i) *castanea* and *chlorotis* are of similar size; (ii) the sub-antarctic teals are substantially smaller than the others and with *nesiotis* being approximately 20% smaller than *aucklandica*; (iii) there is greater sexual size dimorphism in the sub-Antarctic teals (26 - 30% cf. 10 -14% for other two); and (iv) the three island forms have reduced wings and the sub-Antarctic teals are flightless.

In all four forms there is a linear relationship between bill length and tarsus length and body mass, and the relationship holds also for *gibberifrons*. But a similar relationship does not hold for wing length (Figure 1); the wing length of *chlorotis* falls midway between the flighted and non-flighted forms. Wing bones of the now extinct Chatham Island population of *chlorotis* were shorter than those of New Zealand birds (P. Millener pers.comm.) and although this form was probably not functionally flightless, wing reduction was apparent.

Ecological characteristics

The principal ecological trends in the move to insular life involve a change in diet consequent upon a change in habitat, and a change in reproductive rate.

HABITAT AND FOODS. Although all four teal occupy freshwater habitats (Table 1), *castanea* and *chlorotis* show a tolerance of brackish and estuarine waters and the animal foods therein (Frith 1977, Norman & Mumford 1982, Norman & Brown 1988,

Weller 1974, Hayes & Williams 1982) and the sub-Antarctic forms have extended their exploitation to the marine foreshore (Weller 1975a,1980, Williams 1986).In the absence of ground predators (and probably competitors - the diminutive but now extinct *Euryanas finsci* was abundant in New Zealand's post-Pleistocene wetlands and forests becoming almost flightless during this period (Worthy 1988)), *chlorotis* also exploited occluded swamplands and swamp forests (Buller 1888,Guthrie-Smith 1927). It became more dependent on invertebrates and detrital foods and adopted a more cursorial or terrestrial habit in the process, an adaptation also very evident in the two sub-Antarctic forms and for which Livezey (1990) has identified skeletal changes.

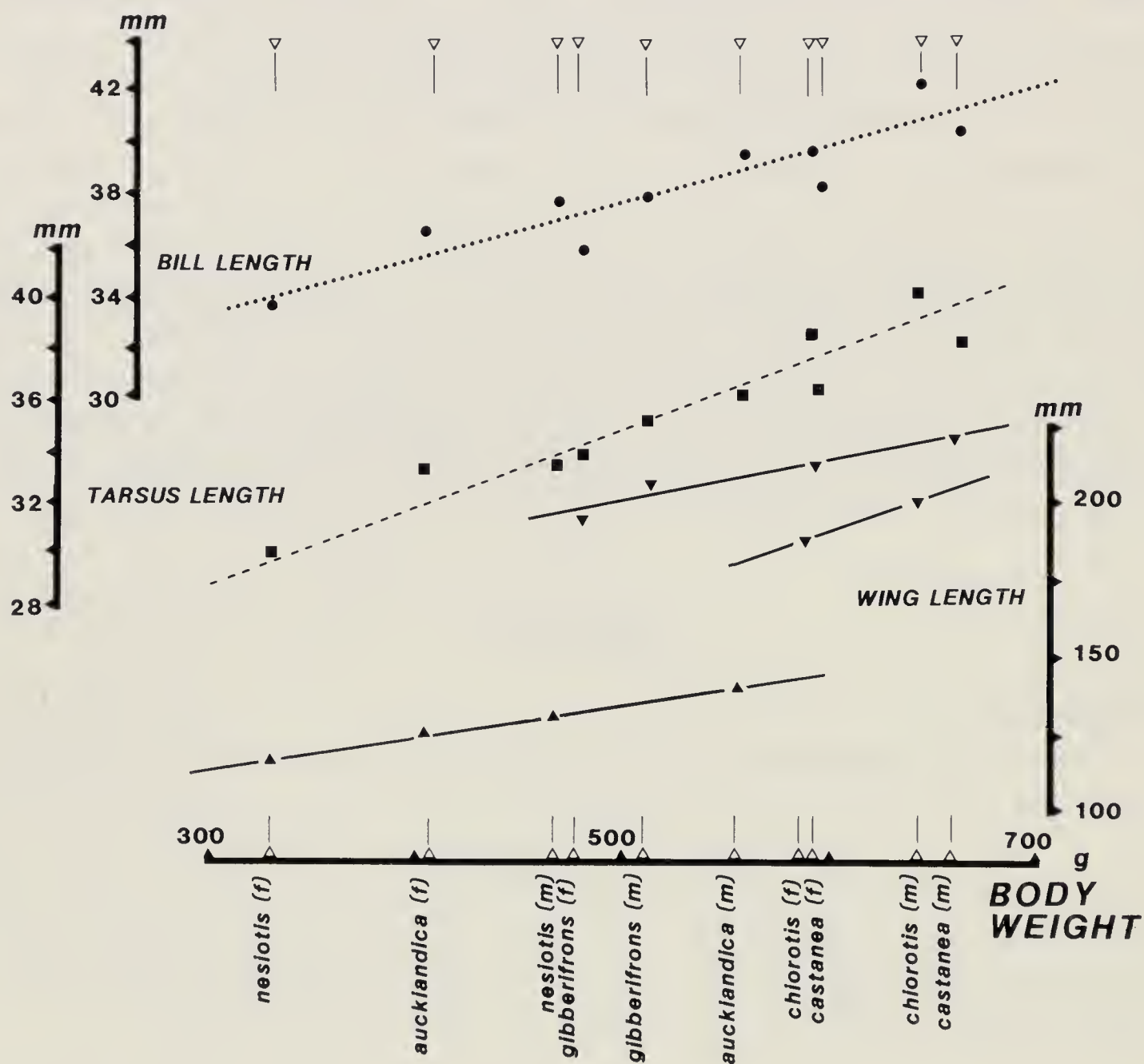


FIGURE 1 – Mean field body weights and measurements of Austral teal. (Source: unpublished data of authors and G. S. Dumbell).

METABOLIC RATES. Accompanying the change in diet, from the generally omnivorous (*castanea*) to the almost exclusively carnivorous (*aucklandica*) are changes in basal metabolic rate (BMR). Brian K.McNab (pers.comm.) has measured these and compared them with predictions from Aschoff and Pohl's (1970) equation for non-passerines: *castanea* had a lower BMR than predicted while those of the other three forms were above predicted values. Relative to their body weights the BMR of *chlorotis* and *nesiotis* were similar (and 9 - 12% higher than the Australian bird) but that of *aucklandica* was 10% higher than *nesiotis*, perhaps implying an adaptation to life on the Auckland Islands which is not paralleled at Campbell Island (for the past 200 years *nesiotis* has been confined to the tiny tussock-clad Dent Island without direct access to marine foods).

TABLE 1 – Summary of the principal habitats and foods of Austral Teal. Number of * indicate relative importance to each species. Sources of data are listed in text.

HABITAT	SPECIES		
	<i>castanea</i>	<i>chlorotis</i>	<i>aucklandica</i>
Brackish lagoons	**		
Estuaries	**	*	
Lakes	*	*	*
Creek mouths	*	**	*
Swamp forests	*	***	*
Hinterland		*	**
Marine shoreline			***
FOODS			
Leaves/shoots	*		
Seeds	**	**	
Estuarine fauna	***	**	
Land invertebrates	*	**	**
Marine invertebrates			***

REPRODUCTIVE RATE. Field data confirm a reduction in clutch size from continental to island forms associated with which is an increase in egg size, a longer laying interval, a longer incubation period and an increase in the size of ducklings at hatching.

Each of the nine eggs in the average *castanea* clutch weighs 7.4% of the female’s body weight, and the total egg material laid (391g) is about two-thirds of her body weight. Eggs are laid daily, the incubation period is 25-26 days and the hatchling emerges weighing 28g, about 64% of the fresh egg weight (Norman 1982) and 4.7% of the female’s body weight.

For *chlorotis* each of the six eggs in the average clutch is equivalent to almost 10% of the female’s body weight, and total egg weight (367 g) is about 60% of the female’s weight (Reid & Roderick 1973, Dumbell 1987).The laying interval is 1.4 - 1.7 days and incubation extends for 27-30 days (Reid & Roderick 1973) while the hatchling weighs 40 g, about 63% of the fresh egg weight and 6.3% of the female’s body weight (S.Anderson pers.comm.).

Each *aucklandica* egg is 18% of the female’s weight, higher than for any other waterfowl (Lack 1968, Rohwer 1988), and the total clutch (4 eggs, 300 g) is equivalent to 74% of female weight. In captivity eggs are laid at 2-3 day intervals, and birds have incubated for in excess of 30 days(n=4) (one artificially incubated clutch hatched after 35 days – S. Anderson pers.comm.). The hatchling weighs 48 g, 64% of the fresh egg weight and 11.7% of the female’s body weight.

No data are available for *nesiotis*: the nest, eggs and ducklings of this form have yet to be observed!

There were conspicuous differences in growth rates of ducklings raised in captivity (Figure 2). Despite being proportionately smaller at hatching, *gibberifrons* and *castanea* ducklings grew faster than *chlorotis*, perhaps indicative of a response to the

more variable continental environment. However *aucklandica* ducklings were considerably different: they hatched 70% heavier than *castanea* and developed faster so that they were half adult weight after 32 days (37 *gibberifrons*, 41 *chlorotis*) and were over 90% of adult body weight at 61 days.

Behavioural characteristics

SOCIAL SYSTEM. Chestnut Teal from several catchments flock together on the larger lakes and estuaries during autumn and winter and disperse to small wetlands and their breeding territories in the spring (Frith 1977). In these winter flocks pair bonds are established, reinforced and challenged but it is not known if bonds persist beyond a single season. Males are intolerant of conspecifics around the nest box in which the mate is laying but paired males attempt extra-pair copulations. Males usually accompany their female and brood actively contributing to parental care. There is no attempt to hold a fixed and exclusive territory during brood-rearing (Norman & McKinney 1987).

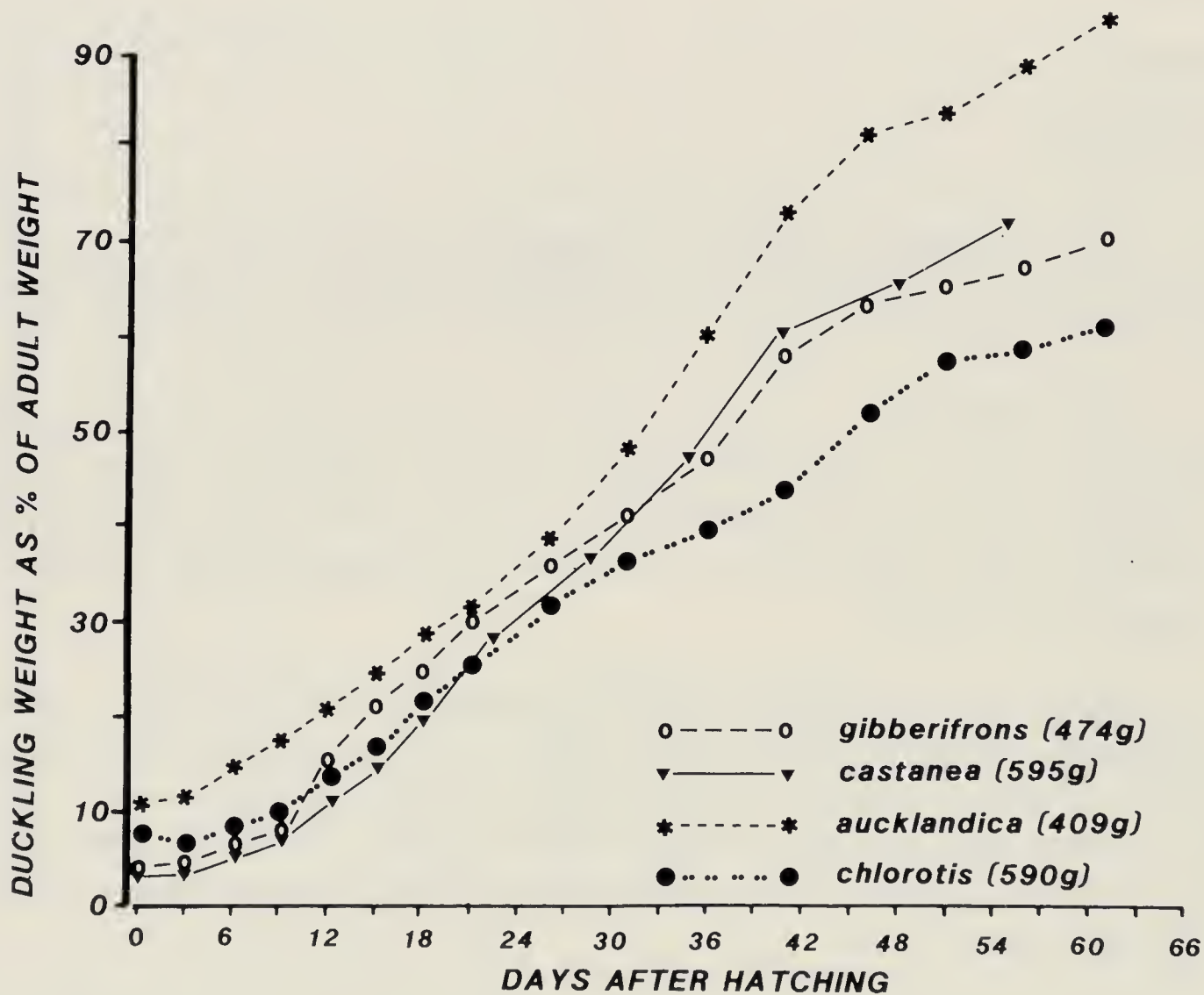


FIGURE 2 – Growth rates of Austral teal ducklings raised in captivity. Ducklings of *aucklandica*, *chlorotis* and *gibberifrons* were raised as broods of three in identical conditions in New Zealand; *castanea* ducklings were raised in larger broods in Australia. The mean weights of females used in this presentation were: *castanea* 595 g; *gibberifrons* 474 g; *chlorotis* 590 g; *aucklandica* 409 g.

Brown Teal are more sedentary, seldom dispersing beyond the immediate catchment (Hayes & Williams 1982, Dumbell 1987). However, they show seasonal changes in population dispersion, forming communal roosts at traditional sites in late summer to mid-winter and occupying small exclusive breeding territories in the spring. Dumbell (1987) reported that most birds in these flocks are unpaired until a month or two prior to breeding but his data suggest that some pair associations persisted beyond a single season. Paired males attempt extra-pair copulations and contribute to parental

care for most of the fledging period during which time the brood is confined to the breeding territory (Dumbell 1987).

In contrast, Auckland Island Teal are dispersed as pairs on exclusive territories throughout the year (Williams unpubl.), unpaired or non-territorial individuals forming small flocks in protected bays (Weller 1975a, Williams 1986, Moore & Walker 1990). All activities including nesting, brood rearing, feeding and moulting appear to be confined to this small territory. Males contribute parental care although they are not regularly seen close to the brood (Williams unpubl.).

COURTSHIP BEHAVIOUR. Social courtship in *castanea* is similar to that of many *Anas* ducks, with a full repertoire of male displays (Johnsgard 1965, Prawiradilaga 1985). Males group around a single female on the water, maneuver to position their bodies broadside to the female, and direct displays at her. Grunt-whistle displays are often followed in tightly-linked, stereotyped sequences with other displays (Head-up-tail-up + Turn-toward-female + Bridling + Nod-swim), and males tend to perform Down-up displays synchronously. Courting parties may take wing from time to time and courtship flights follow.

In *chlorotis*, courtship is less obvious, occurring on water and on land and mostly at dawn and dusk (McKinney, in press, unpubl.). The most striking feature of courting bouts is the predominance of vigorous chasing and fighting between competing males; the birds appear very tense and displays are inconspicuous and infrequent. The display repertoire differs strikingly from that of *castanea* in the following ways: (a) Grunt-whistles are performed singly rather than linked in display chains; (b) Head-up-tail-up and Down-up displays appear to be absent from the adult male repertoire, occurring only as relicts in juveniles; (c) Ritualised comfort movements (e.g. Bill-dip, Drink, Preen-dorsal) are very frequent and often performed in well-defined sequences; (d) Jump-flights and courting flight appear to be absent.

Although courtship behaviour of the sub-Antarctic teal has not been studied in detail, we suspect social courtship is either absent or very inconspicuous. Overtly hostile displays such as Chin-lift, Open-bill threat, rushes and chases characterised autumn social interactions of *aucklandica* on Ewing Island (Williams unpubl.) and Weller (1975a) considered the conspicuous Trill was a male threat display. Introductions of a female to captive *aucklandica* and *nesiotis* males elicited intense male male hostility (rushes and fights), prolonged Trills, and several ritualised comfort movements (Preen-behind-wing, Bill-dip, Drink, Wing-flap) from males and Nod-swims, Inciting and Decrescendo calls from the females.

DISCUSSION

By treating the four Austral teal as a sequence from continental to island forms (*castanea-chlorotis-aucklandica/nesiotis*), six trends are apparent. There is: (1) a reduction in body size and a disproportionate decrease in wing length leading to flightlessness; (2) a change in diet from an omnivorous habit to an apparent dependence on animal foods; (3) increased exploitation of terrestrial habitats and a more cursorial gait; (4) a shift in breeding strategy from the r-selected to the K-selected; (5) a change in social organisation from the seasonally social and dispersive to one

where pairs are dispersed year-round on fixed and exclusive territories; (6) the loss of conspicuous courtship displays and long display sequences and the greater use of more subtle displays derived from comfort movements.

Islands, particularly small cold-temperate ones, are generally inhospitable for pioneering waterfowl. They have low floristic diversity, a restricted range of habitats and generally oligotrophic wetlands (Tyler 1972). Successful colonisation may depend on a predisposition or an established ability to accept mostly animal foods from the maritime environment. As Hochbaum (1946) and Lack (1970) have pointed out, *Anas* ducks are very successful pioneers because of their mobility, non-specific diet and high reproductive rate and *castanea* has the additional attribute of being able to adapt to high salt loadings (Baudinette et al. 1982)

Exploitation of an island's coastal resources imposes a carnivorous component to the diet, a physiological consequence of which appears to be a higher metabolic rate. Ways to compensate for this could involve either an increase in thermal insulation efficiency or a reduction in body size so that although food intake per gram of body weight increases, total food intake is reduced. Reduction of body size may lead to flightlessness, particularly where the need for flight (for seasonal migration, predator escape, or seasonal dispersion of food) is diminished and a reduction of the flight muscles has adaptive value.

Energetic constraints may also contribute to the change in reproductive rate. Some predominantly insectivorous/carnivorous anatids lay their eggs slower than the egg-per-day rate which appears typical of many omnivorous/herbivorous *Anas* species, e.g. at 2-3 day intervals in *aucklandica*, and at 2 and 6-8 day intervals resp. for the riverine insectivores *Hymenolaimus malacorhynchos* (Williams 1991) and *Merganetta armata* (Moffett 1970, Eldridge 1986). The reduction in clutch size may reflect this increased feeding and metabolic effort but it may also be influenced by another selective force - the need to ensure maximum duckling survival. Proportionately heavier ducklings hatch from *aucklandica*'s larger eggs and they probably have a reduced period to homeothermy (Koskimies & Lahti 1964) as well as a shorter fledging period (Figure 2). This may ensure better post-hatching survival in the cooler sub-Antarctic latitudes where sudden icy squalls occur throughout summer. A similar argument has been advanced by Mehlum et al. (1987) who regard increased egg size and reduced period to homeothermy and fledging in some procellariiformes as an adaptation to cold. The cost of producing a larger egg with greater nutrition for a more advanced hatchling is a smaller clutch.

The behavioural differences between continental and insular Austral teal appear related to (1) variation in exploitation of terrestrial habitat, and (2) the spatio-temporal predictability of resources. Both *chlorotis* and *aucklandica* feed more extensively on land than *castanea* (and *nesiotis* is now restricted to terrestrial habitat), behaviour that may be a response to the less diverse but generally more predictable island environments they inhabit, reducing their need for flying and promoting the use of relatively small home ranges. Localisation of resources has favoured their defense - seasonally as exclusive breeding territories by *chlorotis*, as year-round territories by *aucklandica*. Selection for aggressiveness has apparently accompanied this spatial organisation and promoted greater sexual size dimorphism.

Selection for aggressiveness in these species may also have moulded their display repertoires (McKinney in press). The long chains of conspicuous displays used by *castanea* are unlikely to be effective in *chlorotis* and *aucklandica* because of the likelihood of disruption of the chains by fighting and chasing among rival males. More subtle displays derived from comfort movements are probably less provocative to rivals, and furthermore they are more suitable for performance on both land and water. The absence of aerial courtship in *chlorotis* and *aucklandica* is consistent with their highly terrestrial habits, and other modifications in display repertoires may be related to the needs of crepuscular and nocturnal signalling.

This brief appraisal of the Austral teal shows them to be a remarkable group. Every taxonomic assessment emphasises their close relatedness, sufficient to suggest a common and recent ancestor. Austral teal now occupy, for the most part, contrasting niches on the Australian continent (Frith 1977) and have colonised all large and small islands downwind of the continent. Within this group flightlessness appears to have evolved twice, and another island population (Chatham) may have had reduced flying ability. They have come to occupy diverse habitats over a wide range of latitudes, adopting different feeding habits and modifying their social organisation and behaviour in the process. Their further study, and that of other continental *Anas* with remote island derivatives (e.g. *A. acuta* (Stahl et al. 1984), *A. platyrhynchos*, *A. georgica* (Weller 1972, 1975b)) may help elucidate the ways in which ecological factors shape social systems and behavioural repertoires.

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CONCLUDING REMARKS: ECOLOGICAL AND BEHAVIOURAL ADAPTATIONS OF SOUTHERN HEMISPHERE WATERFOWL

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Many fascinating problems relating to the ecology and behaviour of southern hemisphere waterfowl were revealed decades ago by the pioneer studies of Frith, Braithwaite, Kear, Siegfried and Weller. This symposium shows that progress is being made in addressing some of these problems, although in most respects we are still hampered by lack of basic information. Nevertheless, enough work has been done to indicate promising directions for research, and some questions can now be more precisely defined.

Earlier interest in the factors that trigger breeding in Australian waterfowl has lead to new questions about the adaptations of arid-zone species. A general point that has emerged is the importance of dry-land flooding (rather than “a rise in water levels”) in producing the flush of invertebrate food that stimulates breeding.

A study of White-cheeked Pintails at the northern edge of the species' range in the Bahamas raises intriguing questions about *Anas* social systems in the tropics. In this population, pair-bond duration is variable, non-breeding is common, and polygyny occurs regularly. These characteristics could be related to sedentary life, extended breeding seasons, low availability of invertebrate food, variable female body condition, and variable mate quality. Comparative work on other populations at different latitudes and experimental tests of specific causal hypotheses are needed.

Exciting new findings on various aspects of the behaviour and ecology of New Zealand's river-dwelling Blue Duck were presented in this symposium. A 10-year study on individually marked birds has yielded nearly complete data on demography, genetic relationships, and recruitment for one population. This makes the Blue Duck one of the most thoroughly investigated species of waterfowl, an achievement possible only because of its sedentary habits. The discovery of strict genetic monogamy in breeding pairs is especially significant in view of the prevalence of extra-pair copulations in most duck species. This provides support for the hypothesis that strict monogamy is associated with the strong development of territoriality in all four river ducks. Further work is now needed to test hypotheses on the factors that favour territoriality in these species.

Male parental care is unknown in northern hemisphere dabbling ducks but it is well developed in certain southern hemisphere species. It appears, however, that males have three options - to desert, to contribute parental care, or to accompany brood females without providing care. Much basic field work is needed to determine costs and benefits of these male strategies, and to assess vulnerability of ducklings to predation in different habitats.

In spite of the great mobility of waterfowl it may still be possible to reconstruct speciation events in particular cases. Preliminary work on Austral teal illustrates the great heuristic value of a convincing phylogenetic hypothesis. More biochemical analyses of anatid phylogeny are badly needed to provide a sound basis for studies of evolutionary changes in social systems.

Symposia limited to a single avian family are rare at this congress but the restriction allowed us to focus on specific aspects of adaptive radiation in a meaningful way. Inter-hemispheric comparisons are very helpful in revealing ecological correlations and in providing a broadly balanced view of the phylogenetic constraints that have been important during the evolution of this widely distributed group of birds.

SYMPOSIUM 13

THE AVIAN FEEDING SYSTEM

Conveners W. J. BOCK and P. BUHLER

SYMPOSIUM 13

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SOMATIC MODIFICATIONS OF FEEDING SYSTEM STRUCTURES DUE TO FEEDING ON DIFFERENT FOODS WITH EMPHASIS ON CHANGES IN BILL SHAPE IN OYSTERCATCHERS

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ABSTRACT. Bill shape and prey choice are closely associated in the European Oystercatcher *Haematopus ostralegus*. Individual birds usually specialize on the same few prey types from one year to the next while retaining the same shape of the bill. Upon a change in food the bill shape adapts to the new prey chosen. This leads to a temporary decrease in rate of prey capture and handling efficiency. The cost of changing feeding specialization may be particularly high when cold spells suddenly and drastically change food availability.

Keywords: Oystercatcher, *Haematopus ostralegus*, bill shape, prey choice, thickness bill tip, feeding specialization.

INTRODUCTION

Do individual feeding specializations pay? According to Partridge & Green (1985) positive evidence comes primarily from (1) studies on changes in gut morphology in response to changes in digestibility of the food (see also Sibly 1981) and (2) studies of changes in foraging efficiency with experience. Not mentioned is that adaptive modification of the feeding apparatus may also be linked with feeding specializations. This is suggested by seasonal changes in bill length associated with changes in food observed in some passerines (ref. in Hulscher 1985) and changes in bill shape associated with changes in prey choice or feeding technique published for the European Oystercatcher *Haematopus ostralegus* (Swennen et al. 1983, Hulscher 1985), the Great Tit *Parus major* (Gosler 1987) and the Nuthatch *Sitta europea* (Matthysen 1989). As part of our attempt to understand the costs and benefits of feeding specializations in the Oystercatcher we summarize existing knowledge, our own field observations and experimental work on (1) the association between bill shape and food choice and (2) the significance of the thickness of the bill tip in opening large bivalves. In another paper we investigate to what extent other characters of the bill predispose individuals to particular feeding specializations (Hulscher & Ens unpublished).

STUDY AREA AND METHODS

This paper is part of an ongoing study on the behavioural ecology of a breeding population of Oystercatchers on the island of Schiermonnikoog in the Dutch Wadden Sea. From 1983 onwards we captured all unmarked birds on the nest to colour mark them and take biometric measurements. When a marked bird was recaptured in a later year we again took all biometric measurements.

The main observation area consisted of about 600 x 600 m² of mudflats adjoining the saltmarsh, partitioned by stakes in 50x50 m² sites. Two observation towers were positioned on the edge of the saltmarsh and one on the mudflat in the centre of the grid. During the breeding season the whole observation area was scanned once a week for the presence and location of colour marked birds, which were followed until at least one prey item was eaten. With the use of 20 x 60 telescopes the species of nearly every prey item could be identified successfully, except for some very small ones. In all, about ten thousand prey captures by 200 individual Oystercatchers were observed from March - July 1986 to 1989.

RESULTS

How modifiable is the bill tip?

We measured thickness of the bill tip to the nearest 0.1 mm with vernier callipers at 3 mm from the extreme end of the tip. Birds with a thick bill tip that were recaptured in later years tended to have a thick bill tip again (Figure 1): 52% of the changes were within error range of measuring; however, 48 % of the changes exceeded this range and must have been real.

TABLE 1 – Change in bill shape at recapture.

Shape at first capture	Shape at recapture			
	N	Pointed	Intermediate	Blunt
Pointed	26	65.4%	34.6%	–
Intermediate	131	12.2%	66.4%	21.4%
Blunt	140	1.4%	35.0%	63.6%

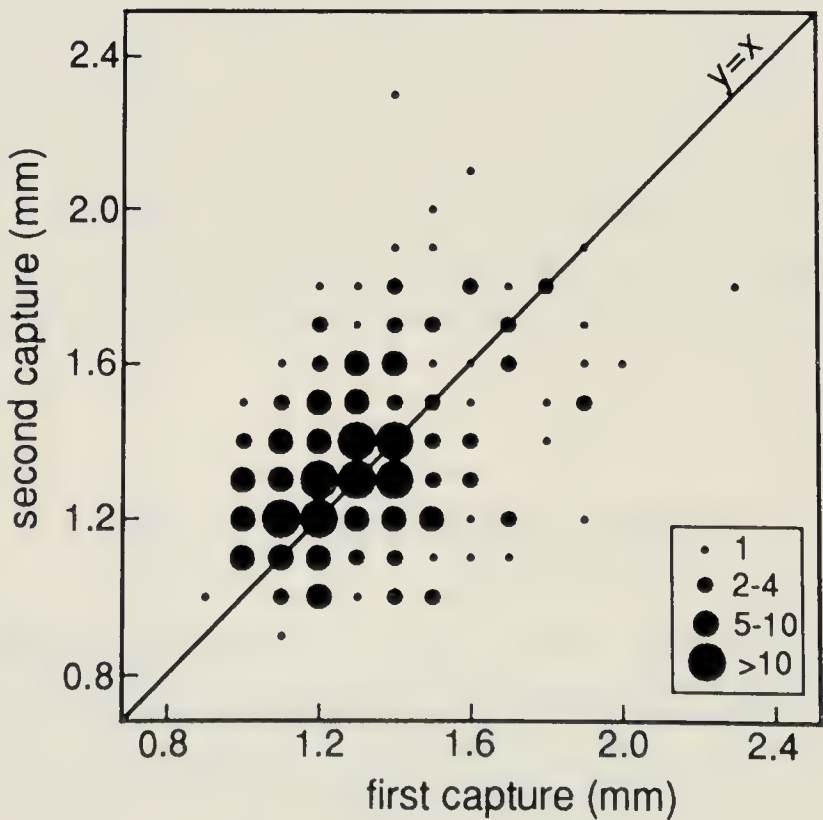


FIGURE 1 – Correlation diagram of thickness of the bill tip at first and second capture (r=0.39, n=296 , P<0.0001).

Following Hulscher (1985), the shape of the bill tip in lateral view was classified in three categories: pointed, intermediate and blunt. The boundaries between the categories were not sharp, but generally there was good agreement between observers in classification (see also Swennen et al. 1983). About two-thirds (Table 1) of the birds had kept their original bill shape when recaptured, irrespective of the initial category. As may be expected, the majority of the changes observed were alterations in shape from intermediate into pointed or blunt or vice versa.

In conclusion the recaptures indicate that bill shape and thickness are modifiable as demonstrated by Swennen et al. (1983) and Hulscher (1985). It is also clear that in most cases bill shape did not change and thickness did not change much. In the following we will attribute this to the tendency of individuals to prefer the same prey in subsequent years.

How consistent is prey choice?

In our study area only four prey species were sufficiently abundant to become the staple food of individual Oystercatchers: *Macoma balthica*, *Nereis diversicolor*, *Mya arenaria* and mussels *Mytilus edulis*. The first two prey species were by far the most important. The percentage of any one of these staple foods in the diet of individual birds was positively correlated to the percentage of that prey in the diet in the following year (Table 2). The pattern of prey choice consistency can also be presented in another way when we define that an individual specializes on a particular prey if more than half its diet consists of that prey. Table 3 shows that the majority of individuals specialized on the same prey in consecutive years.

TABLE 2 – Consistency of prey choice: correlations between the proportions of one prey species in the diet of individual birds in two consecutive years (* $P<0.01$, ** $P<0.001$).

Years	<i>Nereis</i>	<i>Macoma</i>	<i>Mytilus</i>	<i>Mya</i>
1986 to 1987	0.72**	0.75**	-	0.37*
1987 to 1988	0.72**	0.47**	0.70**	0.16
1988 to 1989	0.81**	0.74**	0.02	0.32

TABLE 3 – Consistency of prey choice: the proportion of individuals specializing (50% or more in the diet) on the same prey species in two consecutive years.

Years	<i>Nereis</i>	<i>Macoma</i>
1986 to 1987	62% (16/26)	76% (19/25)
1987 to 1988	66% (19/29)	72% (26/36)
1988 to 1989	100% (4/ 4)	83% (10/12)

Are bill shape and prey choice associated?

We added all prey captures over all years for all birds having the same bill shape and calculated the proportion of each prey in the diet of the various groups (Table 4). Birds with pointed bills took significantly more *Nereis* and *Mya* and significantly less *Macoma* and *Mytilus* than birds with blunt bills.

TABLE 4 – Composition of the diet in relation to bill shape.

Prey species	Bill shape		
	Pointed	Intermediate	Blunt
<i>Nereis</i>	62.4%	38.8%	22.7%
<i>Mya</i>	10.6%	7.5%	4.4%
<i>Arenicola</i>	1.7%	1.3%	0.7%
<i>Carcinus</i>	0.3%	0.5%	0.5%
<i>Cerastoderma</i>	0.7%	1.9%	1.8%
<i>Macoma</i>	23.2%	45.9%	59.7%
<i>Mytilus</i>	1.1%	4.2%	10.1%
Total prey	1024	3754	4602

Thickness of bill tip in relation to opening large bivalves

Oystercatchers open large bivalves like mussels and cockles either by stabbing or hammering. When stabbing, the bill is forced between the valves and the adductors are severed. No damage to the shell occurs. When hammering a hole is made in one of the valves by a series of hard blows with the bill tip. Individuals usually keep to one technique, but some may perform both (Durell & Goss-Custard 1984, Goss-Custard & Sutherland 1984, Sutherland & Ens 1987). To gain entry into the prey, stabbers need gaping mussels. Hammerers can open closed mussels. Circumstantial evidence (Swennen et al. 1983) suggests that the thickness of the bill tip is linked to the technique chosen: stabbers having a thin, hammerers a thick tip. Precise measurements in the field are lacking.

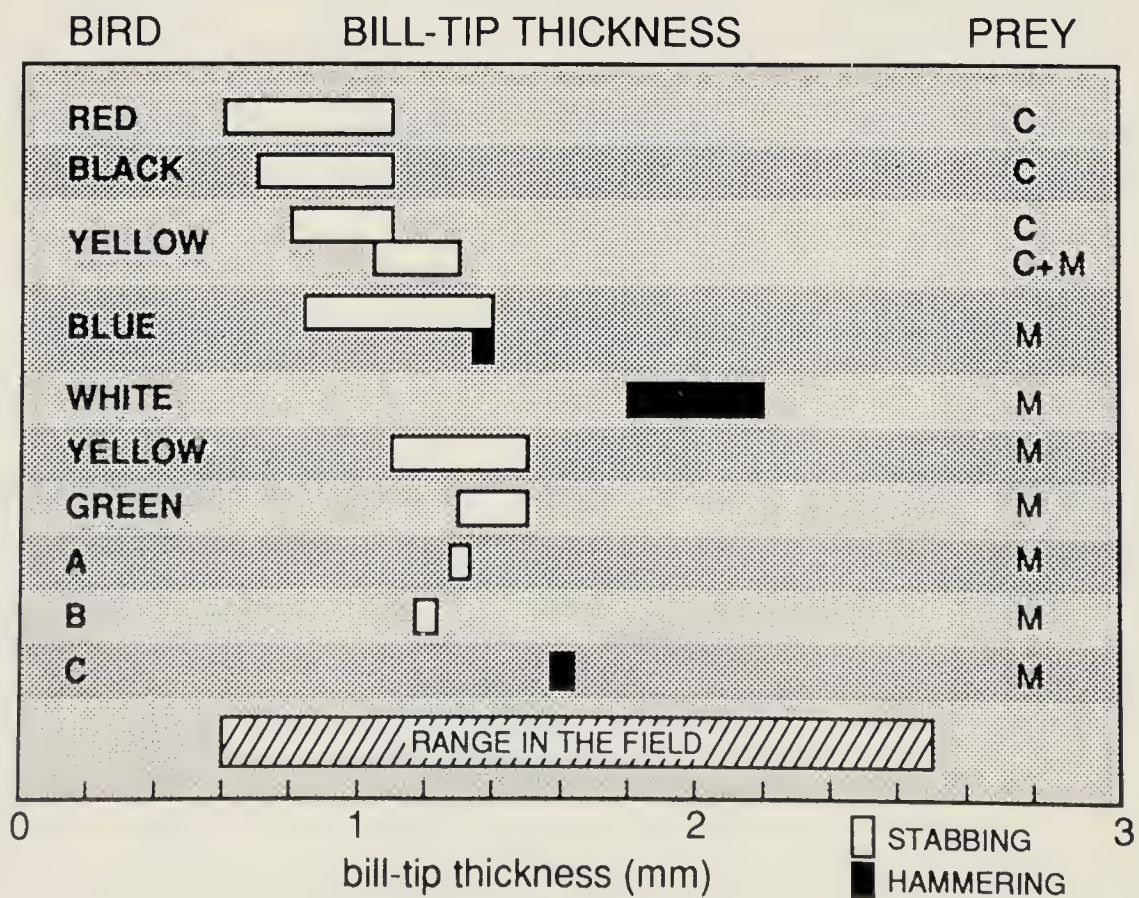


FIGURE 2 – Range in thickness of the bill tip of captive individual adult Oystercatchers and their way of opening cockles and mussels either by stabbing or hammering. From top to bottom: Red to White when feeding in cages on semi-natural prey populations (Swennen et al. 1983), Yellow and Green in the laboratory with a small number of mussels in sea water on offer (Hulscher in prep), A to C in cages on a natural musselbed (Hulscher 1985).

From 1987 onwards our study area included a small musselbed, so it is not surprising that mussels comprised only 7% of the total diet of the Oystercatchers: 25% of all birds were seen eating this prey while most of them also took other prey. Among the mussel-eaters stabbers prevailed: 90% of these birds always stabbed, whereas 10% usually hammered, but some individuals performed both techniques. Birds that at least once hammered a mussel had a bill tip that was significantly thicker than birds that only stabbed (hammerer: 1.38 mm, SD=0.18, N=22; stabber: 1.28 mm, SD=0.17, N=184; $t=2.59$, $P<0.01$). However, the difference was small, which may be due to the fact that only very few individuals hammered mussels all of the time.

Scanty, but precise information on tip thickness and feeding technique is available from captive birds (Figure 2). Most were stabbers and the thickness of the bill tips of individual birds varied within rather narrow limits. The range for the whole group of stabbers was from 0.60 to 1.50 mm and for the three hammerers from 1.34 to 2.20 mm. The behaviour of bird Blue (Swennen et al. 1983) was interesting. When it had been feeding on sands with only worms for a week and having a pointed bill with a tip 1.35 mm thick, it was transported to a musselbed. Ten days later, as shown by observations, its pointed bill tip had been transformed into a truncated one, while the mussels were opened by hammering (tip thickness was not measured). A few weeks later the bird was seen hammering and stabbing; its tip was then 1.35 to 1.40 mm thick. Still later only stabbing occurred while the tip became thinner, varying between 0.85 and 1.20 mm.

Experimentally altering tip thickness.

Clearly, bill shape and bill tip thickness adapt to prey choice and feeding technique. The important question confronting us is whether individuals also become more efficient when the bill tip becomes adapted to their preferred prey and feeding technique. Circumstantial evidence that this may be the case is presented for *Macoma* by Hulscher (1982) and for *Mytilus* by Sutherland & Ens (1987). Here we report preliminary results obtained from one adult Oystercatcher experimented upon in the laboratory. The bird was allowed to feed on mussels in sea water while its behaviour was documented on video. It opened the mussels by stabbing and the thickness of its bill tip remained constant at 1.5 mm (Figure 3). When this pattern was sufficiently clear we removed the extreme 2.5 mm of the bill by a fast rotating grindstone. During the next three weeks, observations continued while biometric measurements on the bill were frequently taken.

After the manipulation the bird continued to open the mussels by stabbing. However, its total handling time, averaged over the first 12 days following the manipulation, increased significantly ($P < 0.01$). Opening time was two times longer ($P < 0.01$), whereas eating time was only slightly longer ($P < 0.1$). Even more important is that the bird seemed seriously hampered in successfully opening mussels by stabbing: only 10 % of attacks were successful, compared with 59 % successful attacks before the experiment.

DISCUSSION

Our data show a clear correlation between prey choice and bill shape and between feeding technique and thickness of the bill tip. Prey choice itself may be determined by other factors like the length and/or strength of the bill (Hulscher and Ens in prep.,

Swennen et al. 1983) and will not be discussed. Here we first review the evidence that a change in diet precedes a change in bill shape. Next, we investigate why a particular prey choice leads to a particular bill shape. Finally, we discuss the costs of changing feeding specialization imposed upon the Oystercatcher by the adaptability of its bill tip.

Does bill shape dictate food choice or vice versa?

The first indications we had that shape alteration follows upon a change in food was by considering Oystercatchers wintering in the Wadden Sea when they return to the inland breeding areas. Upon arrival nearly all birds have blunt bills, which all change into pointed ones within 2-3 weeks. This coincides with a change in food, consisting of bivalves on the coast to soft-bodied prey inland (Hulscher 1985). Later, Swennen et al. (1983) demonstrated experimentally that changes of pointed bills into truncated ones (with alterations in the tip thickness) indeed occur in a couple of weeks within the same birds when they feed on worms or bivalves respectively. Gosler (1987) and Matthysen (1989) also found adaptive changes of bill form upon changes in food within individual Great Tits and Nuthatches respectively.

Changes in prey choice may be expected if a change in feeding area is involved. This usually happens after the breeding season when feeding is no longer restricted to the breeding territories. Change of feeding area may occur only locally or on a larger scale, for instance during migration. For the birds at Schiermonnikoog one third showed a change in bill shape when retrapped within breeding seasons (Table 1). Retraps in the non-breeding seasons are not available. For another site in the Wadden Sea (Paesens) at 10 km distance from Schiermonnikoog they are available. Of the retraps 44% showed change of shape within breeding seasons, 62% within non-breeding seasons and 61% between breeding and non-breeding seasons (Hulscher 1985).

Bill shape and prey choice

We have seen (Table 4) that a pointed bill was associated with *Nereis* feeding and to a lesser extent with *Mya* and *Arenicola*. *Nereis* and *Arenicola* live in up to 25 cm deep permanent burrows. They are soft-bodied animals that need not be prepared in a special way before swallowing as hard shelled prey do, like molluscs and crustaceans. Sometimes, however, worms are washed before they are eaten. *Mya* is a filter feeding clam, having its siphons fused in a thick fleshy envelope that can be extended extremely far up to the mud surface. Due to the large depth of the shell Oystercatchers usually only eat the siphons by tearing them out of the shell. If the shell is within reach of the bill it can be opened easily, because the shell gapes permanently at its posterior end, also when the siphons are retracted into the shell.

Oystercatchers breeding inland mainly feed on soft-bodied prey like earthworms, leatherjackets and caterpillars. They all have pointed bills and the extreme 2 cm of the rhamphotheca of all shows lateral wear (Hulscher 1985). Lateral wear on the tip never occurs among Oystercatchers feeding in the intertidal. Thus, a pointed bill originates through abrasion around all sides of the tip while probing for soft-bodied prey. Only in a tough substrate, like inland pastures, where penetration of the bill can only be achieved by forceful sideways movements of head and bill, lateral forces operating on the bill tip crack and abrade the horny covering.

A blunt bill is particularly associated with the eating of mussels and cockles. The cockle is a moderately sized (specimens up to 40 mm shell length are eaten) bivalve that lives only half a centimetre beneath the surface. Mussels can be eaten up to 70 mm shell length. They live on top of the sands. Both mussels and cockles can close their shells firmly.

When opening a mussel or cockle by stabbing, the extreme end of the bill is brought into the slightly gaping shell by surprise. Further penetration into the shell is achieved by forward pushing and sideways levering movements of head and bill till the adductors are reached and can be severed. During the opening phase strong sideways forces are operating on the extreme tip of the bill. A pointed bill, characterised by a small depth and usually also by a small width (Swennen et al. 1983), probably is too weak to withstand the lateral forces. Small pieces may break off the bill till a truncated (blunt) tip is formed that can withstand greater sideways forces due to its greater depth. The blunt form of the bill probably originates only during the opening of bivalves, not when the flesh is removed from the shell after opening. Captive Oystercatchers retained their pointed bills when fed with thawed mussels gaping widely (Hulscher 1985).

Intermediate bill shape was associated with feeding on *Macoma* and *Nereis*. *Macoma* is a small bivalve (up to 24 mm shell length) that lives moderately deep from 2 to 10 cm. It can be opened by biting through pressing the tips of the mandibles on the shell margin (Hulscher 1982). *Scrobicularia*, a relative of *Macoma* (larger, up to 45 mm), is also regularly eaten by Oystercatchers. It is a deep dwelling species with moderately small adductors. To open a *Macoma* or a *Scrobicularia* probably requires less effort and can be achieved with a less high bill tip. An intermediate bill arises when friction forces between bill and substrate during probing obliquely abrade the outer corners of the mandibles, while the inner corners remain truncated as a prerequisite for opening relatively weak bivalves like *Macoma* and *Scrobicularia*.

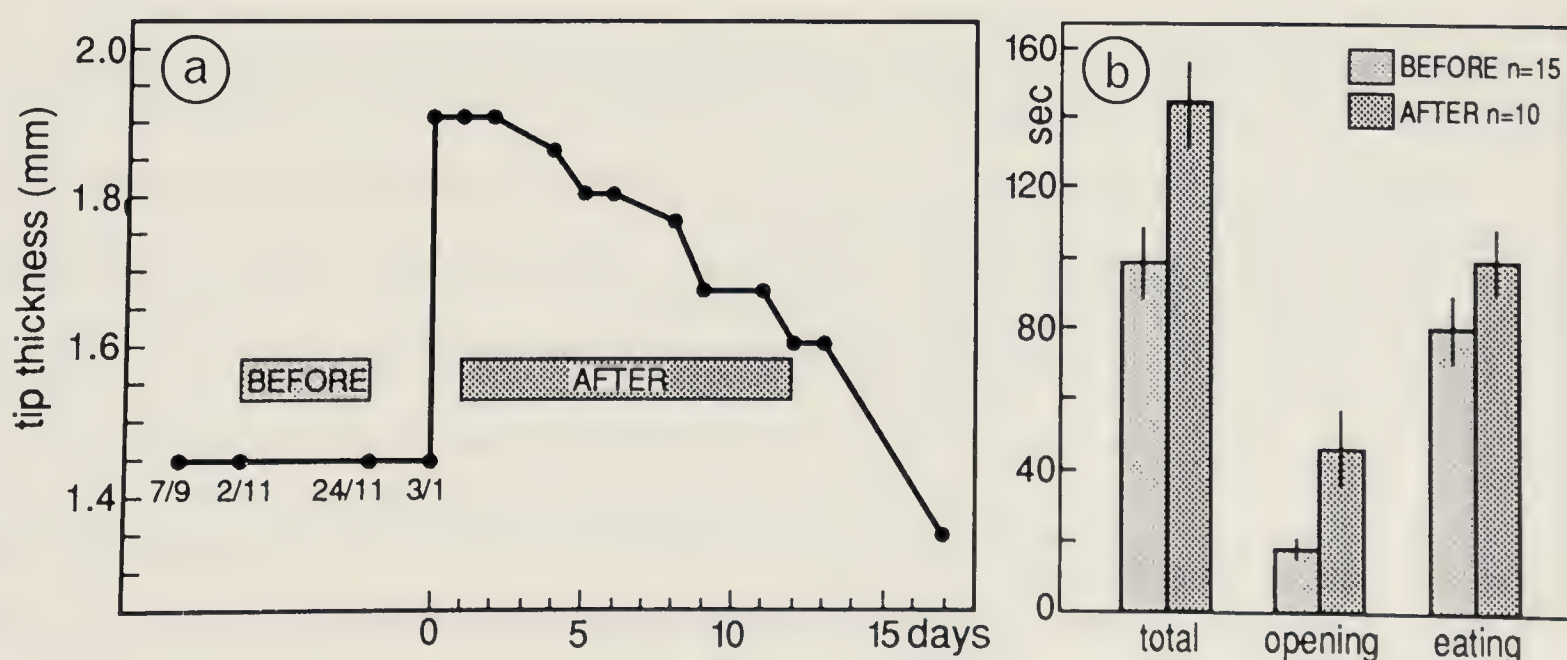


FIGURE 3 – a) Change in bill-tip thickness of an adult Oystercatcher feeding on mussels in the laboratory. On 3 Jan., the thickness of the tip was experimentally altered (see text). b) Total handling time (mean \pm SE) and its components opening and eating time per successfully opened mussel before and after the manipulation of tip thickness.

The cost of changing feeding specialization.

When Oystercatchers change their diet they are temporarily hampered in feeding on the new prey till the shape has become adapted (Figure 3, and Swennen et al. 1983). The cost of this change depends on the duration of the changeover period and the magnitude of the decline in efficiency in handling and capturing prey animals. Our experiments indicate that assessing the latter under more natural conditions is within reach. Because of the formidable growth rate of the bill of the Oystercatcher (0.4 mm per day), necessary to compensate the likewise formidable rate of abrasion (Hulscher 1985), the duration of the changeover period amounts to only two weeks (Figure 3). Under normal conditions this may not pose a great strain on the birds. Changes in feeding conditions, however, can be sudden and dramatic during cold spells, when the energy needs of the birds are maximal and the availability of the different prey species may be differently affected. High leveled intertidal flats which particularly harbour moderate and deep-dwelling prey get frozen more easily than low leveled flats. Birds accustomed to feed on the former are more often forced to move. During severe winters intertidal cockle populations can be completely wiped out. *Macoma* is a well, *Mytilus* a moderately cold resistant species. During cold spells large-scale redistributions of Oystercatchers take place, usually accompanied by mass emigration and mass mortality (Hulscher 1989). Under such conditions selective mortality among food specialists may be expected.

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RECOGNITION OF FOOD IN PECKING, PROBING, AND FILTER FEEDING BIRDS

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ABSTRACT. Food recognition during avian pecking is controlled by specific food characters. Food recognition mechanisms in trophic specialists (probing sandpipers -*Calidris*; filter feeding ducks -*Anas*, and flamingoes - *Phoenicopterus*) are modifications of this basic mechanism, because of its plastic design and flexible motion patterning. These modifications result from insertion of new behavioral patterns at the transition of head approach and intra-oral food transport. Insertion of touch-controlled food-gathering patterns is accomplished by reorganization of touch organs. Reorganization results either in use of refined and more rapid tactile recognition of food via size and hardness, or in development of a new tactile capacity via vibration of prey. Both modifications require a smooth transfer of motor control from one sensory input modality (vision) to another sensory input (tactile).

Keywords: Food recognition, trophic diversity, pecking, filter feeding, probing, vision, taste, touch, *Columba*, *Gallus*, *Anas*, *Phoenicopterus*, *Calidris*.

INTRODUCTION

Where foraging ends feeding begins. Many studies on avian foraging consider feeding as a black box. However, foraging models must be combined with food processing models to understand how release from morphological constraints and behavioral innovation may occur in evolution of the avian feeding system. Changes in food recognition are of primary importance here. Therefore, a comparative analysis of cues in food recognition is initiated in this paper to characterize plasticity in the avian trophic design.

Pecking behavior is a common feature of avian feeding in all Neornithes. Pecking behavior is characterized by specific head, jaw, and tongue motions that occur in well defined subsequent behavioral phases: head fixation, head approach to food, grasping food, and intra-oral transport. To characterize the generality in food recognition while pecking, neurosensory control must be studied in taxons in which pecking is not obscured by other specialized feeding mechanisms. Berkhoudt (1985) and Zweers (1985) have shown that pigeons *Columba* and chickens *Gallus* meet this criterion. These authors mainly discussed mechanical aspects, but decisive for evolutionary change are the relationships between sensory cues, recognition performances and feeding morphology. We first describe the common pecking design for food recognition.

Then we examine several trophic specialists. Differences these specialists exhibit in food recognition compared with the general pecking mechanism may elucidate what kind of specifications determine plasticity of the avian feeding design. Therefore, a comparison of sensory cues and organs, and recognition performances is undertaken in some selected trophic specialists, filter feeding in ducks *Anas* and flamingoes *Phoenicopterus*, and probing in sandpipers *Calidris*. In particular, we focus on

food-recognition systems controlled by touch and taste, because they vary considerably, but are basic to all forms of pecking.

PECKING IN PIGEONS AND CHICKENS

Recognition during head fixation and head approach

The basic pecking pattern has been described in detail elsewhere (Zweers et al. in prep.). It need be summarized here as framework to describe food recognition. Alternate static and dynamic phases occur. Exteroceptive information is gathered during static phases to initiate adequate motor patterns in the subsequent dynamic phase, carefully refined by proprioception about the initial position of the muscle-bone apparatus. Pecking starts with the "head fixation phase" during which the head is kept a few cm above the food, during which position and size of the food object are determined by vision. Next follows a depression of the head; meanwhile the beak opens and the eyes close. This motion can not be interrupted once initiated. The "head approach phase" is vision-controlled and characterized as follows. The beak tips move continuously along the shortest path to the food grain. Gape size correlates with seed size (Bermejo et al. 1989). Vision also controls location of the food-directed peck, but during the final head depression, vision is no longer involved in adjusting motion, so that it becomes a ballistic open loop control (Schall 1989).

Recognition during beak grasp and intra-oral transport

As head approach ends next phase is the "food grasping phase". Then follows either a drop by beak opening, rejection, headshaking, re-positioning or re-testing by small catch and throw motions, or intra-oral transport. The "intra-oral transport phase" is either a catch and throw mechanism, a lingual wet adhesion mechanism, or a combination of the two. Initiation and subsequent release of these patterns are under control of food size, hardness, taste and position along the jaws. These releases are characterized as follows. Small seeds are transported by lingual wet adhesion, while larger ones are moved by catch and throw, or by a combination of the two. When clay balls are offered, non-alert birds transport them to the lingual base, before rejecting them, while alert birds reject them at the beak tips. The same was found in pigeons and chickens when seeds were acid (Berkhoudt 1985).

Touch and taste

Pigeons and chickens possess four types of mechano-receptors lying dispersed in the oral mucosa: Herbst corpuscles, Grandry corpuscles, Merkel corpuscles, and free nerve endings (Berkhoudt 1985, Gottschaldt 1985). Gentle & Breward (1986) have described a bill tip organ of about 20 dermal papillae densely packed with corpuscles of Herbst, and Merkel/Grandry corpuscles in the horny nail of the chicken's lower beak. This organ plays a role in the discrimination of food, as do the taste buds, which lie in the oral mucosa adjacent to the sides of the tongue and along more caudal palatal and lingual base areas (Berkhoudt 1985). The mechano-receptors input to a trigeminal-CNS feeding circuit that controls the various feeding patterns in birds, similarly information of the taste buds is relayed by the facial nerve (Dubbeldam 1984).

FILTER FEEDING IN WATERFOWL AND FLAMINGOES

Recognition during filter feeding in *Anas*

RECOGNITION CAPACITIES. Filter feeding is an extension of pecking (Zweers et al. in prep.). The head approach phase is vision controlled, but that ends once the beak tips are submerged; subsequent control of head and jaw motion is taken over by the touch system in a way different from that in pecking. This is illustrated as follows. Filter feeding in ducks is performed by two mechanisms (e.g. Kooloos et al. 1989): 1) A suction-pressure pump mechanism that sucks suspensions of kernels in at the beak tips and expels the water along the more proximal jaw rims. (2) A filtering mechanism which retains kernels by either one of two mechanisms or a combination of the two: Sieving is the one mechanism acting by "direct interception" of kernels and lamellae. This "food-recognition" mechanism is mechanical; it is dominant in Shovelers. The mesh width directly determines minimal size of filtered food. "Inertial impact deposition" is the other mechanism acting by centrifuging kernels out of vortices that develop along the lamellae; this mechanism is also mechanical, it is dominant in Mallards and Tufted Ducks if they strain small kernels (< 4 mm). For larger kernels the direct interception mechanism works. Kooloos et al. (1989) have shown that beak kinematics during filter feeding keep lamellar mesh widths and beak gapes carefully adjusted to the seed size offered, which results in maximal intake performance. Such flexible adjustment of the pumping and filtering mechanisms requires primarily a continuous measuring of food size at the mouth entrance. Two other recognition features need to be mentioned that additionally require a very fast feedback for gape-size adjustment. First, Mallards and Tufted Ducks are able to exclude larger seeds from smaller while straining. Second, Mallards are able to strain peas in preference to soft clay balls randomly submerged in wet sand (50 peas are eaten in 60 s while 50 clay balls are left without any imprint).

TOUCH AND TASTE. Such highly adjustable feeding patterns thus must possess high discrimination capacities and must rely upon highly sophisticated detection apparatuses, decoding units, and patterning in CNS-premotor centers. Waterfowl have a highly specialized bill tip organ which is built as follows. In the horny nail of both maxilla and mandible in waterfowl, half circular rows of small keratin caps cover dermal touch papillae that run in tubules through the horny nail. These papillae are filled with mechano-receptors, a cluster of 10 to 20 Grandry corpuscles distally and 5 to 15 Herbst corpuscles proximally (Berkhoudt 1976, 1980, Gottschaldt 1985). These papillae function in tactile discrimination by direct touch (Zweers 1985). They allow size and hardness recognition by integrating e.g. upper and lower beak tip input via a strongly enlarged trigeminal-CNS feeding circuit.

Recognition during filter feeding in *Phoenicopterus*

RECOGNITION CAPACITIES. In Caribbean Flamingoes, filter feeding is an extension of pecking comparable to that of ducks. Flamingoes have a high food-size discrimination capacity controlled by touch; however, this is accomplished in a way different from waterfowl. Flamingoes have a water transport mechanism that primarily pumps suspensions in and out along the same major route (e.g. Jenkin 1956). Suspensions are sucked in and expelled along the lateral jaw rims. Retention of kernels is a highly sophisticated system: exclusion of particles was found by Zweers and De Jong (in prep.); e.g. grass seeds (2.8 mm) were exclusively ingested from a mixture with larger green peas (4.8 mm), which were excluded. Retention by sieving was found; e.g. in

a mixture of broken millet (1.4 mm) and grass seeds (2.4 mm) all grass seeds were collected while the smaller millet was washed away.

TOUCH AND TASTE. Gape-size adjustment requires a food recognition system equally sophisticated as described in ducks; however, the touch-recording apparatus must lie along the lamellae rather than more distally at the beak tips. Dissection confirms that dense networks of branches of Ramus mandibularis as well as R. ophthalmicus trigeminis project to Herbst corpuscles along the lamellar bases. The distribution of taste buds in flamingoes and ducks looks more clumped than in pecking birds (Berkhoudt 1977, 1985) in which screening and selection of food occurs along a more continuous route. It is noteworthy that in flamingoes condensed areas of taste buds lie in the oropharyngeal mucosa along the glottis. In ducks, however, a densely packed taste bud area lies along the roof of the oropharynx in the caudal palate (Berkhoudt 1977, 1985). It is tempting to correlate the inverted position of these sensory fields functionally with the inverted head position during filter feeding in flamingoes.

PROBING IN SANDPIPERS

Recognition during probing in *Calidris*

RECOGNITION CAPACITIES. Probing in waders is also a modification of the basic pecking mechanism. The head approach phase is again vision-controlled and non-interruptable once released. The beak, however, exhibits a small, fixed gape. But, as soon as the slightly opened beak tips touch the substrate, subsequent bill penetration is under control of touch. This tactile control acts quite differently from that in pecking, since any change in head motion may occur. Repetitive head depression and elevation patterns develop, namely probing (Gerritsen 1988). If the beak tips strike a prey while probing, the rhynchokinetic beaks open, and the prey is grasped and pulled out. Then, the basic mechanism of intra-oral food transport is released. In addition to this food recognition by direct-touch hunting, Gerritsen & Meyboom (1986) have shown that Sanderlings too have the capacity for "remote-touch hunting". These authors have calculated, from preference experiments, that the probability of direct hits upon prey hidden in the substrate is far too small to have directed the selection of the best foraging location. They estimate that prey detection even occurs when at two or even more centimetres from the tips.

TOUCH AND TASTE. Starting from the requirement of a "remote-touch" capacity, Zweers et al. (1991) have proposed a food recognition mechanism for Sanderlings feeding upon Nerine sized prey given: (1) A moldable beak tip; and (2) Presence of sufficient touch corpuscles of Herbst, Grandry and/or Merkel. They have shown that only Herbst corpuscles can be involved and that neither organization as a facets-touch organ (acting like a facet-eye), nor as a fields-touch organ (acting by measuring phase-shift or difference in arrival time of travelling waves produced by moving worm) meet the "remote-touch" condition. However, a clusters-touch organ comprising only corpuscles of Herbst, and that operates via measuring differences in intensity of passing waves, meets remote-touch condition. They calculated that a minimum of 150 corpuscles of Herbst organized in at least 15 clusters (10 corpuscles each) at both beak tips would meet the "remote-touch" condition. This prediction is confirmed by observations of microsections of bill tip organs in Sanderlings and other Scolopacidae; total counts

are above the minimum values (Bolze 1968, Gerritsen 1988). In addition to Herbst corpuscles, only Goglia (1964) mentioned presence of Grandry corpuscles.

Sandpipers possess a dense field of taste buds along the oral mucosa at the level of the lingual tip and the caudal palate. These fields comprise many more buds than in the studied pecking birds, and they lie also somewhat more caudally. These observations parallel data from Gerritsen (1988) and co-workers. They investigated gustatory stimuli and concluded that Sandpipers direct their probing activities according to these stimuli. Combining requirements from penetration, grasping of burrowed prey, remote touch, and increased gustatory capacities clearly requires increased density of enlarged taste bud fields, shifted somewhat caudally (Zweers et al. 1991).

COMPARISON OF VISION AND TOUCH CONTROLLED FEEDING

It was shown that the behavioral elements of head approach (vision-controlled) and intra-oral food transport (taste-and touch controlled) during pecking are retained in such trophic specialisms as filter feeding and probing (touch-controlled). The major food-recognition differences between these specialized feeding techniques and the basic pecking mechanism are that new highly sophisticated touch-controlled behavioral patterns are developed at the transition of vision-controlled head approach and touch-and-taste controlled intra-oral transport. In fact, jaw, tongue, and head motions of the basic pecking mechanism are re-patterned by introducing either (1) a much refined and rapid recognition of food characters like size and hardness (e.g. ducks); or (2) a new ability to recognize vibration (e.g. sandpipers). These sensory stimuli are monitored by an extended and increasingly complex trigeminal input system at the beak tips. Taste organs were shown to adapt primarily to requirements of effective monitoring positions. These changes fit in the control models developed by Zweers (1985) and Schall (1989) for pecking as refined extensions in touch recording/decoding units, and as interpolating/re-patterning motor units.

Comparisons of food recognition during the basic pecking mechanism and the derived specialisms lead to the conclusion that the design of the pecking mechanism – if it is considered as the ancestral avian feeding mechanism (cf. Zweers et al., 1991) – has a remarkable plasticity, while its motor-patterning is highly flexible. Two specific capacities that accomodate change are: (1) Re-organization of available tactile monitoring mechanisms (e.g. direct-touch) into refined or new ones (e.g. remote-touch) that implement earlier non-discriminated food characters (e.g. waves traveling in mud); (2) Connection of these re-organized mechanisms and new motor patterns making a specific feeding behavior more effective. Implementation of this feature is observed when change in external conditions, like penetrating mud, initiates a transfer from discrete vision into continuous touch control of head-and-jaw motion.

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ECOMORPHOLOGY AND AVIAN FEEDING BEHAVIOR

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ABSTRACT. The ecomorphology of avian feeding behavior has been examined by a wide range of approaches which cross traditional boundaries of ornithological research. These approaches parallel the major forces which influence avian phenotypes. Feeding behavior and associated morphological tools are affected by mechanical (functional), evolutionary, ecological, and behavioral forces. The avian phenotype, in turn, affects the future action of these forces, creating an intricate system of biological feedback. An understanding of avian feeding behavior demands a recognition of the complexity and interrelatedness of these and possibly other biological forces, just as the subject of ecomorphology recognizes contributions from a diversity of biological researchers.

Keywords: Ecomorphology, morphology, behavior, ecology, evolution.

ECOMORPHOLOGY

Ecomorphology is a relatively new area of biology, even though relevant studies have been carried out for centuries (Bock 1990). James (1985) defines ecomorphology as “an attempt to understand the functional relationship between morphological variation in animals and their ecology.” In practice, studies of ecomorphology in animals, particularly birds, include elements of comparative morphology, ethology, ecology, and evolution (Winkler 1990). We suggest that ecomorphology is not a single approach, but rather the common focus of these and possibly other scientific traditions.

APPROACHES TO ECOMORPHOLOGY

Ecology, in the general sense, concerns the interaction between living organisms and their environment. Extending this definition, ecomorphology concerns the relationship between an organism’s morphology and its environment. Different approaches to ecomorphology (Figure 1) emphasize different aspects of an organism’s “environment.” Here we review examples of these approaches with reference to avian feeding behavior. Our purpose is to help clarify the domain of ecomorphology and to illustrate how ecomorphological studies have contributed to our understanding of avian feeding systems.

Functional approaches

Before ecomorphological relationships can be established, investigators must first understand the form and function – the phenotype – of morphological characters, just as ecologists must begin with an understanding of natural history. Ecomorphological studies of avian feeding behavior often begin with a consideration of the avian bill. Birds display a fascinating variety of bill sizes and shapes, widely recognized for their

role in feeding (McClelland 1979). Detailed investigations have been carried out on a number of specialized taxa. Crome (1985), for example, examined the filtering abilities of four species of Australian waterfowl differing in the distribution and form of their bill lamellae. The Pink-eared Duck *Malacorhynchus membranaceus*, with the most unusual bill morphology, was the most efficient at filtering plankton from an experimental feeding apparatus. Yet Crome’s results showed that relative filtering efficiency among the four species could not be predicted by simply treating the bill as a mechanical sieve. Subtle design features and behavior apparently play key roles in the use of these ducks’ morphological equipment.

Approaches to Ecomorphology

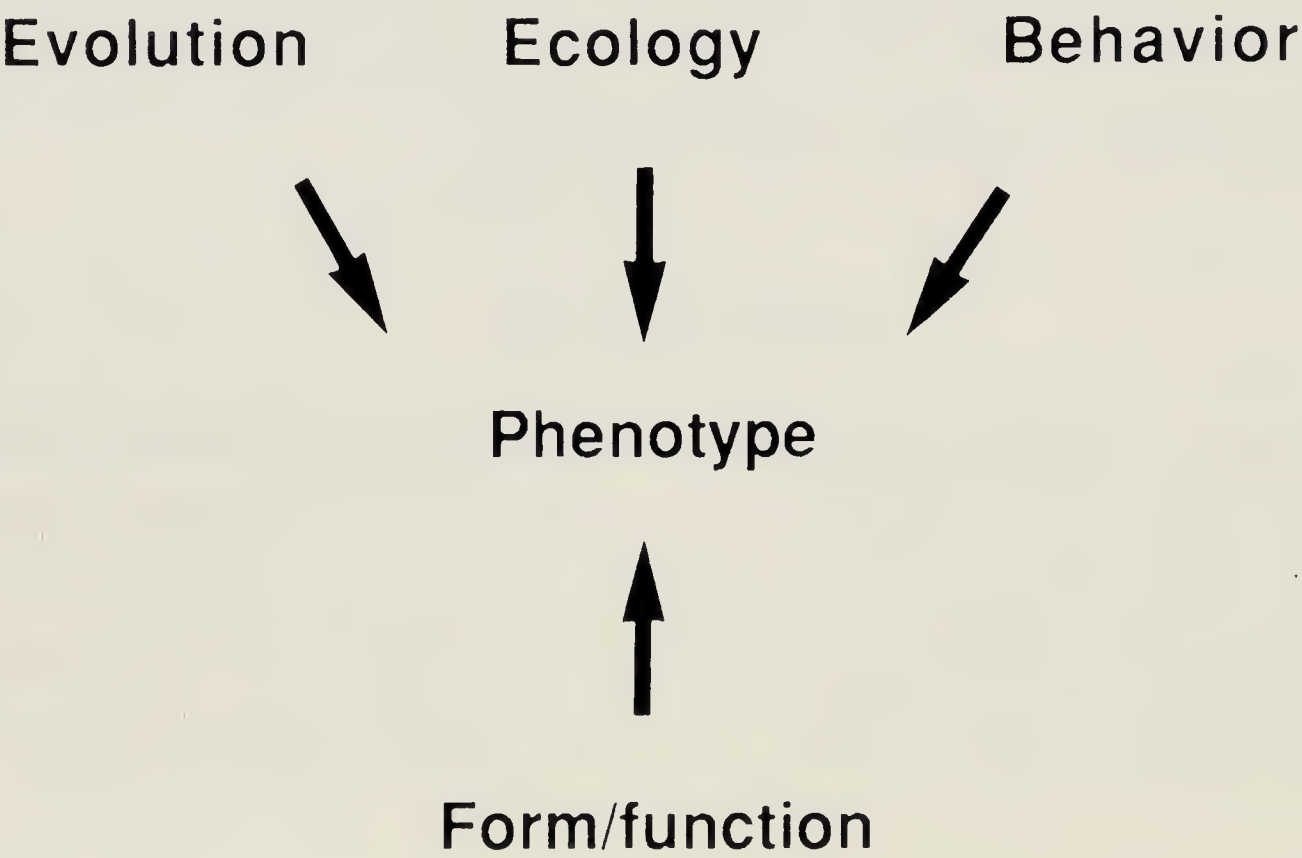


FIGURE 1 – General approaches to ecomorphology which focus on the phenotypes of target species, populations, or individuals.

A classic study by Bock (1966) examined the relationships between size, weight, and physical forces acting on a generalized avian bill. Based on a consideration of mechanics, Bock concluded that specialized bill shapes like the curved bills of seedeaters might be related as much or more to weight reduction as to the optimal design for feeding. Like Crome’s analysis, morphological form was clearly linked to functional aspects of feeding, but only in the context of other, sometimes unanticipated, factors.

Our own work on the feeding behavior of insectivorous passerines has shown that even rather slight differences in bill morphology are associated with differences in feeding efficiency. We compared food handling abilities of captive birds representing five species of North American insectivores, Ovenbird *Seiurus aurocapillus*, Yellow-rumped Warbler *Dendroica coronata*, Palm Warbler *D. palmarum*, Magnolia Warbler *D. magnolia*, and Ruby-crowned Kinglet *Regulus calendula*. The bills of these birds

differ mainly in size (Figure 2). Experimental feeding with different-sized prey (*Tenebrio* larvae) showed that birds with larger bills were able to handle larger prey more effectively. This result applied to individuals of different species (Figure 3) and even to individuals of the same species.






		<u>EXP.</u> <u>CUL.</u>	<u>CUL.</u> <u>WIDTH</u>	<u>CUL.</u> <u>DEPTH</u>	<u>WT.</u> <u>(g)</u>
	OVENBIRD	12.6	4.2	4.7	19.8
	Y. - R. WARB.	10.6	3.9	3.9	11.5
	PALM WARB.	11.9	3.3	3.3	9.6
	MAGN. WARB.	10.3	3.6	3.5	9.5
	R.-C. KINGLET	9.5	3.5	2.4	6.9

FIGURE 2 – Bill dimensions and body weights of captive passerines analyzed in our feeding experiments. Sample sizes were Ovenbird (10), Yellow-rumped Warbler (10), Palm Warbler (5), Magnolia Warbler (8), and Ruby-crowned Kinglet (6).

Bills aren't the only morphological characters that play a role in avian feeding. Specialized hindlimbs and feet provide access to special foods for trunk gleaners (Norberg & Norberg 1990), long-legged waders (Baker 1979), divers, and perching birds (Commisso 1990). Wing morphology of birds such as raptors, fruit-eaters, aerial insectivores, and seabirds can be directly tied to their feeding methods (Pennycuick 1972, Moermond 1990). Raikow et al. (1988) examined the specialized wings of alcids, diving petrels, and penguins. Penguin wings are characterized by highly reduced wing muscles and limited flexion of the major joints. Diving alcids and petrels possess more rigid joints than their non-diving relatives, but their wing mobility and musculature are significantly greater than that of penguins. This analysis illustrates the concept of ecomorphological trade-offs. Flight requires joint mobility and strong flight muscles; as long as flight is retained, the capacity for specialized diving is limited.

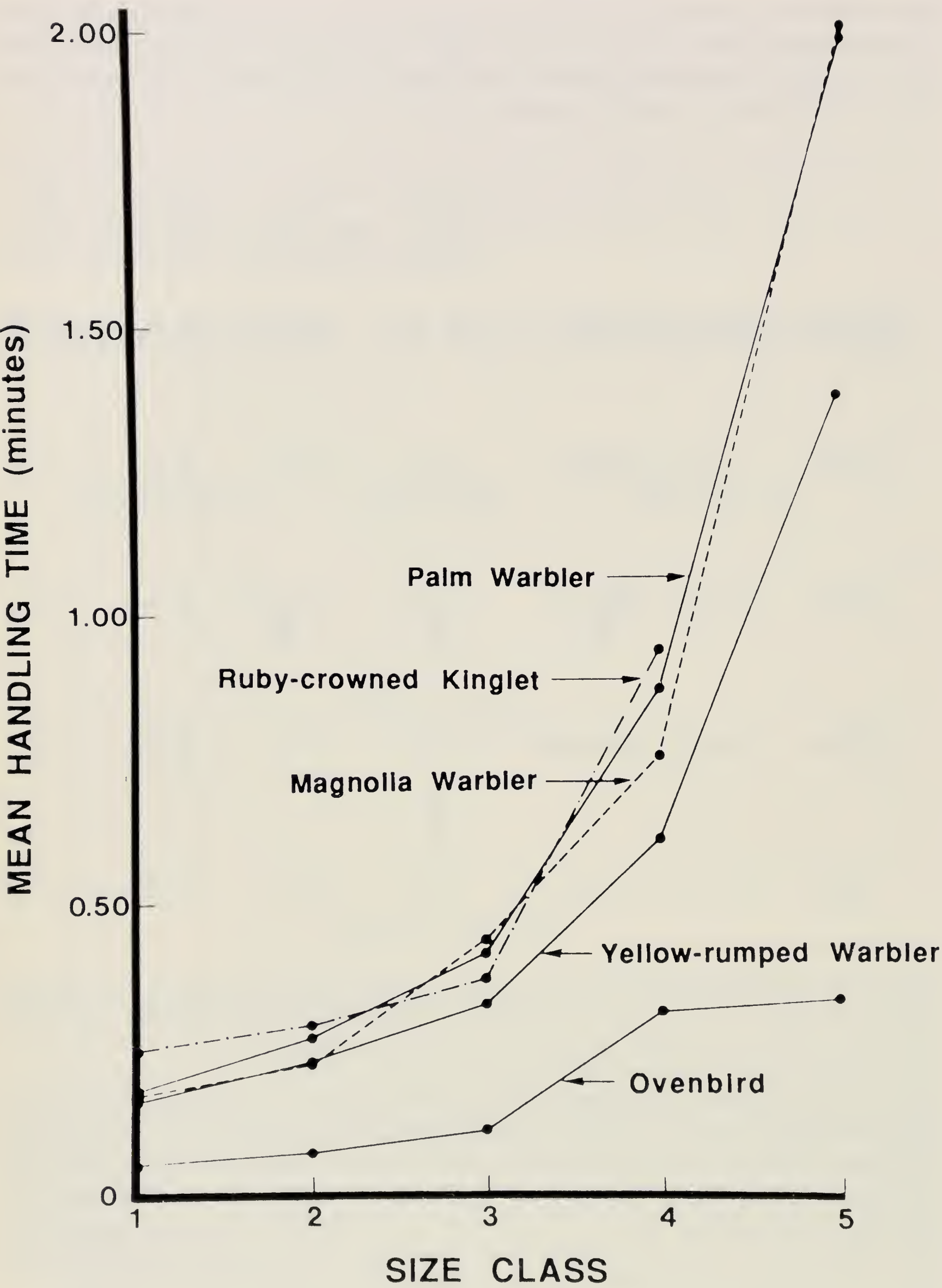


FIGURE 3 – Mean times for handling and consuming *Tenebrio* larvae (mealworms) for bird species shown in Figure 2. More than 200 observations were recorded overall for each species, although sample size varied for each prey category. Observations were < 5 only for Ruby-crowned Kinglets feeding on the largest prey category. Size categories were: 1 = 5-12 mm; 2 = 13-17 mm; 3 = 18-22 mm; 4 = 23-27 mm; 5 = 28-34 mm.

Careful studies of form and function are necessary to avoid mistaken assumptions about morphological adaptations. Lederer (1972), for example, demonstrated by high-speed photography that rictal bristles, previously suspected to be accessory food-gathering structures, serve no direct role in the aerial food capture of several North American tyrannid flycatchers. Such a result serves as a caution against untested assumptions about the functional role of morphological characters.

In summary, analysis of form and function sets the stage for other investigations of ecomorphology. Feeding behavior incorporates many elements of a bird's morphology, elements that in turn may be associated with other activities. In many cases, relationships between form and function are fascinating in their own right.

Evolutionary approaches

Evolutionary forces are particularly difficult to demonstrate, but their importance to ecomorphology is obvious. The power of evolutionary forces is perhaps best illustrated by the morphological diversity of island avifaunas. Spectacular examples include variations in bill size and shape in the Drepaniidae of the Hawaiian Islands (Amadon 1950) and the Geospizinae of the Galapagos Islands (Grant 1986). Processes responsible for these adaptive radiations involve unknown degrees of chance, geographical effects, ecological interactions, and phylogenetic constraints.

Intraspecific polymorphisms in feeding structures illustrate another level of evolutionary divergence. Newton (1967) noted that a difference in bill size of only about 1 mm accounts for significant differences in feeding habits between male and female European Goldfinches *Carduelis carduelis*. The larger-billed males are better able to reach seeds of teasel, an important winter food resource. Evolutionary interpretation of this difference is clouded, however, by the fact that male Goldfinches are slightly larger overall than females, leaving the possibility that feeding differences might have evolved as a consequence of selection on some other size-related trait. Smith & Temple (1982) showed that striking dimorphisms in the bills of neotropical Hook-billed Kites *Chondrohierax uncinatus* are related to bimodal distributions in the sizes of tree snails, the kites' preferred food. In areas where only one type of tree snail is available, bills of the Hook-billed Kites are essentially uniform.

The reciprocal of adaptive radiation, evolutionary convergence, provides further insights into the power and limitations of evolutionary change. Neimi (1984) studied morphological characteristics of birds in peatland habitats of Minnesota and Finland. In both areas, shrub-dwelling insectivores tend to have longer and wider bills than congeners in nearby forests. The opposite is true for seedeaters. Evolutionary changes associated with peatland habitats seem to be consistent between continents, but these changes are not the same for different ecological guilds. Ricklefs & Travis (1980) used multivariate analyses to investigate patterns of morphological convergence in temperate-scrub bird communities investigated by Cody (1974). Results showed that Cody's species assemblages are characterized by a core of morphological types that are generally similar from one area to another, but a significant one-to-one correspondence of species cannot be justified statistically. A similar conclusion was reached by Karr & James (1975) for lowland forest birds of North America, Central America, and Africa.

Several studies illustrate natural selection directly. The general approach has been to evaluate morphological characters in a population before and after a period of

significant mortality. Boag & Grant (1981) and Price et al. (1984) demonstrated that periods of low rainfall on the Galapagos island, Daphne Major, led to significant mortality in the Medium Ground Finch *Geospiza fortis*. On average, adults in the surviving population possessed larger beaks and larger body size than populations prior to low rainfall periods. The authors found that hard seeds were proportionally more common during drought periods, giving a selective advantage to larger-billed birds. Smith (1990) reported age-specific and sex-specific natural selection in the polymorphic African finch *Pyrenestes ostrinus*. Selection for feeding efficiency favors two different bill sizes, each associated with a different seed resource. Unlike studies mentioned above, Smith's results come from populations that have not been subjected to catastrophic mortality.

Just as evolution plays a key role in shaping morphology, so too does morphology help shape the course of evolution. Natural selection can work only within the limitations of available genetic variation. Collins & Paton (1989) noted dramatic differences between the short hindlimbs of hummingbirds and the longer, more robust hindlimbs of sunbirds and honeyeaters. These differences are correlated with differences in foraging method (hovering v perching). Hummingbirds quite likely evolved from swift-like ancestors, whose short legs were adapted for aerial insectivory. This phylogenetic pre-condition might have played a key role in the evolution of hovering behavior in hummingbirds.

Ecological approaches

Most ecological analyses of avian feeding systems are couched in an evolutionary context and, thus, would be equally appropriate for the preceding section. Here we consider "ecological approaches" which emphasize interactions among species or interactions between birds and their physical environment. A good example of the interface between ecological and evolutionary approaches is the widely-debated subject of character displacement. Schluter et al. (1985) provided evidence that character displacement has been responsible for differences in bill shapes among sympatric Darwin's finches. Like many other researchers, they compared the feeding behavior of two species in sympatry and allopatry, but they also evaluated differences in food availability among localities.

Feeding behavior of many bird species is affected by ecological interactions with plants. The size, shape, color, and arrangement of flowers have been related to the characteristics of major pollinators, including nectarivorous birds (Paton & Ford 1983, Collins & Rebelo 1987, and others). Feeding mechanisms of frugivores are likewise interrelated with plant characteristics. Certain frugivores like cassowaries, toucans, and hornbills possess bills that are obviously adapted to a frugivorous diet. Moermond & Denslow (1985) Moermond et al. (1986) have shown that other more subtle morphological characteristics, including body size, wing shape, and hind limb structure, are important ecomorphological elements of this bird-plant interaction. The interaction between birds and plants probably rarely involves a tight, one-to-one relationship between species, but instead incorporates a complex web of interactions involving suites of plants and suites of pollinators or frugivores (Levey 1987).

The influences of physical factors on bird morphology are poorly known but have been demonstrated experimentally by James (1983), who transplanted nestling Red-winged Blackbirds *Agelaius phoeniceus* into distant geographic areas. Her results suggest

that a surprisingly large amount of morphological variation can be attributed to environmental influences.

Behavioral approaches

Behavioral approaches to ecomorphology emphasize the decisions and actions of individual birds. Like the previous categories, this distinction is rather arbitrary insofar as these actions and decisions are influenced significantly by evolutionary and ecological factors.

General links between behavior and morphology have been examined by considering many species simultaneously. Karr & James (1975), Miles & Ricklefs (1984), Leisler & Winkler (1985), Miles et al. (1987) and others have used canonical correlation to compare complex sets of behavioral and morphological variables. Their results illustrate sets of morphological traits (e.g. small size and broad, flat bill) that are associated with sets of behavioral traits (e.g. "hover-gleaning") or feeding station. Wiens and Rotenberry (1980) have warned that general relationships involving many species across broad geographical scales might not apply at local scales of time and space. On the other hand, multivariate approaches are able to avoid spurious generalizations based on a few, well-studied species and, most importantly, they identify subsets of morphological characteristics that consistently link behavior and ecology.

The ways in which a bird's morphological "tools" are used can be modified significantly by instinct and learning. Newton (1967) pointed out that *Carduelis* finches can learn to pull out "fluff" to obtain seeds from thistles, whereas *Fringilla* finches never exhibit this behavior. Moermond (1990) observed that morphologically similar African bulbuls use different methods to obtain fruits. In our aviary experiments, conspecifics with almost identical bill sizes often exhibited significant differences in their abilities to handle food items. Partridge (1976) reported similar individual differences among captive parids. The significance of individual behavioral differences is illustrated dramatically by Werner & Sherry's (1987) study of the Cocos Finch *Pinaroloxias inornata*. This species as a whole exhibits a rather wide range of diet and foraging behavior, but individuals tend to specialize independently of one another. As with ecology, a bird's morphological "equipment" plays a central role in its day-to-day behavior. Newton (1967) and others have noted that birds engage in considerable trial and error feeding when they are young. Specialization apparently emerges as certain food items or foraging substrates yield higher success rates. Partridge's (1976) well-known studies of parids demonstrated that differences in foot structure and bill shape are related to differences in feeding techniques. Moermond et al. (1986) demonstrated experimentally that food choice in Central American frugivores is related to morphological characteristics. Wide-gaped birds with short, broad wings and poorly-developed leg musculature (e.g. trogons) often take fruit while hovering or flying. These species tend to be more selective in fruit choice than birds which feed from perches. This observation is consistent with the idea that fruit choice is determined by the balance between energetic costs and nutritional benefits.

Avian feeding morphology affects many other elements of behavior. Baker (1979) found that morphological characteristics of waders help determine their habitat selection. Long-billed species, for example, feed in a wider variety of microhabitats than do shorter-billed species. Schluter (1984) demonstrated that differences in bill morphology affect social behaviors such as territoriality and flocking in Galapagos finches. The thicker-billed, more granivorous *Geospiza fuliginosa* abandon territories and feed

Ecomorphology of Avian Feeding

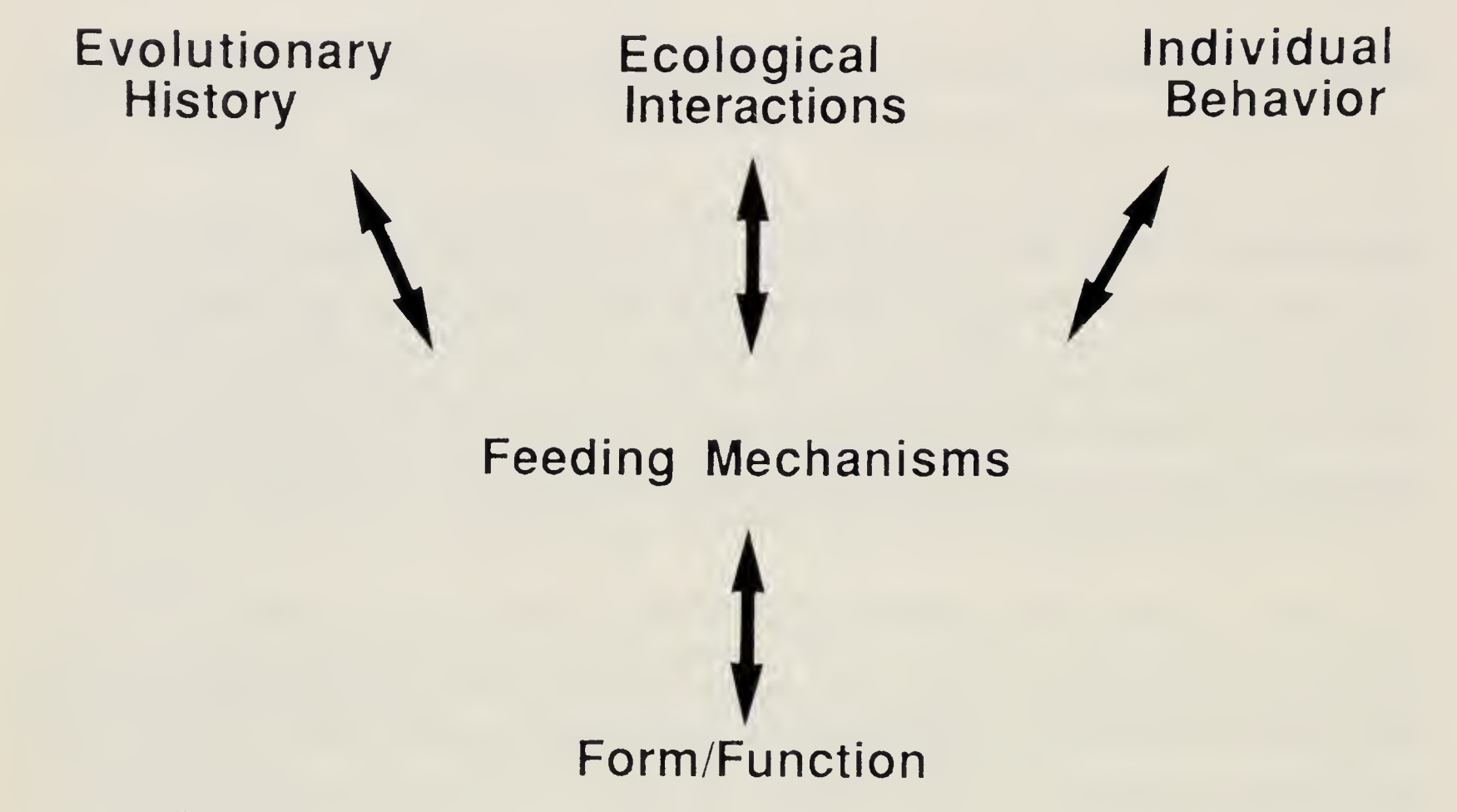


FIGURE 4 – Major forces which influence avian feeding behavior. Note the parallels with Figure 1.

in flocks during the dry season, while the narrower-billed, more insectivorous *G. difficilis* generally continue to feed alone, often in the vicinity their wet season territories. Similarly, Benkman & Pulliam (1988) argued that small North American sparrows have less time available for irregular movements and social interactions than larger finches because the smaller birds must spend more time feeding on smaller seeds.

CONCLUSIONS

We have described a variety of approaches to the subject of ecomorphology. Our categories are neither mutually exclusive nor original (see Sherry 1990). Nevertheless, they encompass a variety of approaches that help us understand ecomorphology in general and avian feeding behavior in particular. These same categories (functional morphology, evolution, ecology, and behavior) can be viewed as important influences on an organism’s phenotype. No one of these influences can fully explain the characteristics of an individual or species. Instead, the phenotype manifests a complex balance among these interrelated forces. The phenotype, in turn, can affect the future direction of these forces, creating a dynamic feedback system (Figure 4). In order to understand avian feeding systems, we must recognize the breadth, complexity, and dynamic nature of these biological forces.

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THE AVIAN DIGESTIVE SYSTEM - AN OPTIMALLY DESIGNED PLUG-FLOW CHEMICAL REACTOR WITH RECYCLE?

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ABSTRACT. "The distinctive features of the avian digestive system are primarily those associated with the development of flight and a high metabolic rate." (Farner 1960). We can restate this observation by Don Farner in a physiological context - the distinctive features of the avian digestive system are high throughput rate, high extraction efficiency, and minimal volume (and associated weight). These are the same properties important when designing an optimal chemical reactor. Because of a unique gastrointestinal reflux exhibited by birds, I would like to suggest that many birds have adopted a chemical reactor design optimized for minimal volume with high yield - the plug-flow reactor with optimal recycle. Using chemical reactor theory, I will examine what new insights are provided on the "optimization constraints" confronting avian digestion, especially as related to efficient assimilation of refractory food items, such as wax esters and chitin.

Keywords: Intestinal reflux, chemical reactor theory, optimal digestion, wax ester digestion, chitin digestion.

INTRODUCTION

"The organization of the avian gastrointestinal tract has been described as being more elegant than that of the straight chain tube system of most fish, but less dignified than that of primates."

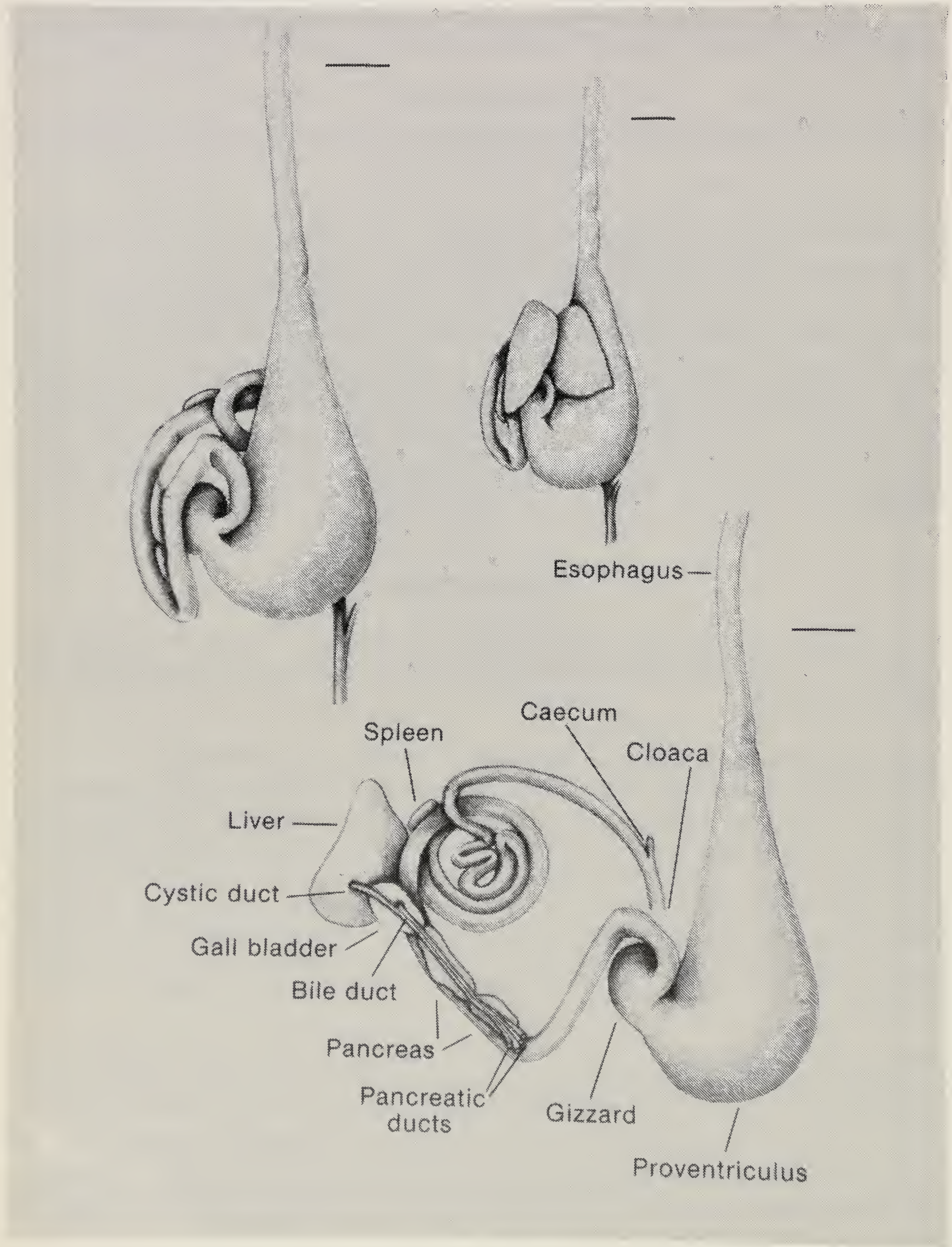
Gastrointestinal anatomy as a determinant of digestive efficiency

Of all avian internal organs, the range of morphological variation in the stomach is the greatest. This reflects both widely differing dietary habits and the importance of the stomach in processing solid food items (Ziswiler & Farner 1972) and food items high in fat (Place et al. 1989). The avian stomach consists of two chambers which are externally distinguishable in most species (McLelland 1979). The glandular proventriculus is continuous with the esophagus and secretes gastric juice. The gizzard or ventriculus is caudal to the proventriculus and functions as the site of gastric proteolysis and, in many species, of mechanical digestion (Duke 1986b).

Less variation is evident in the avian small intestine and rectum. The lengths of various parts of the tract vary with the size of the bird, type of food eaten, and other factors (Ziswiler & Farner 1972). The duodenum is relatively long in birds, comprising some 15-20% of the total length of the small intestine as compared to about 5% in the rat. In the rat, the hepatic and cystic biliary ducts enter the duodenum in close proximity to the pylorus, whereas in the turkey and chick, as well as in many seabirds, the bile and pancreatic ducts enter the distal portion of the duodenum.

The duodenum or proximal intestine is the major absorptive site for many nutrients in birds. For example, nearly 60% of ingested fatty acids are absorbed in the duodenum of turkeys, as compared to 10-30% in the rat (Sklan 1980).

FIGURE 1 - Ventral view of the gastrointestinal tract of 40 day old Leach's Storm-petrel (*Oceanodroma leucorhoa*) chicks.
The scale meter in each view represents 1 cm.



Gastric emptying as a determinant of digestive efficiency

Because the proventriculus and gizzard play a major role in chemical and mechanical digestion of solid food, gastric emptying is a major component of gastrointestinal passage time in birds. In three domestic species (goose, turkey, and chicken), $48.5\% \pm 24.5\%$ ($n = 6$) of the total mean residence time of a meal (7.1 ± 2.25 h) involves gastric emptying (Warner 1981). In Jackass Penguins *Spheniscus demersus* fed fish, 23% of the mean residence time of 11 h involves gastric emptying (Wilson et al. 1985, Laugksch & Duffy 1986). Fish meals are known to empty the stomach more rapidly than meals of squid or krill (Laugksch & Duffy 1986).

Gastric emptying in animals is a highly regulated and coordinated process. Gastric emptying is slow when the stomach contains nutrient-rich food (such as lipids) and is more rapid when the stomach content is less energy rich (such as isotonic salt solutions). In humans, for example, the half-time for gastric emptying of a non-nutrient saline solution is only 7.9 ± 1 minutes while that for a homogenous meal is on the order of 60 minutes (Smith et al. 1984). The stomach is capable of also differentially emptying aqueous and lipid components in a meal. In both humans and dogs, the aqueous phase of a meal empties promptly from the stomach, whereas the solid, extracellular and intracellular fat empty together, in parallel, after an initial lag of nearly 60-90 minutes (Meyer et al. 1986).

We have shown in seabirds that the aqueous components of a meal are emptied from the stomach at a higher rate than lipids. This differential emptying occurs in several species despite striking differences in digestive anatomy. Petrels exhibit a low overall passage rate; gastric emptying comprised 57.8% of the 10.6 h mean transit time for aqueous components and 62.5% of the 20 h mean transit time for lipids. In the penguins only 16% of the 7.5 h mean transit time for aqueous components and 30.3% of the 8.9 h mean transit time for lipids was a function of gastric emptying. Similarly, in Leach's Storm-petrel chicks, the half-time for gastric emptying of aqueous solutions is only 0.35 h while that for neutral lipids is nearly 70 h (Place et al. 1989). Associated with the petrel's low gastric emptying rate is a specialized gastrointestinal anatomy (Figure 1). The petrel proventriculus is relatively large and entire meals reside in the proventriculus for extended periods, as indicated by the low rates of gastric emptying. The function of the proventriculus in procellariiforms, viz thorough chemical digestion of ingesta, is unique among birds. In other species, including penguins, food passes rapidly through the proventriculus and chemical, as well as mechanical, digestion occurs primarily in the gizzard (Duke 1986b).

The pattern of gastric motility in procellariiforms is also unique among birds. The proventriculus is relatively inactive during a digestive contraction cycle in Leach's Storm-petrel *Oceanodroma leucorhoa* chicks. Proventricular contractions are observed only along the ventral surface (Duke et al. 1989). This is in contrast to the vigorous, coordinated muscle activity observed between the gizzard and proventriculus in fowl (Dziuk & Duke 1972, Duke 1982). The inactivity of the procellariiform proventriculus allows gastric lipids and aqueous components to form and remain in separate phases. The denser aqueous digesta accumulates in the ventral portions of the proventriculus and in the gizzard. The pylorus is ventral to the gizzard (and proventriculus) in the petrels and, consequently, aqueous digesta enters the duodenum first while lipid is retained in the stomach. Low gastric motility, slow gastric emptying, and the position of the pylorus relative to the proventriculus result in stomach function analogous to a separatory funnel.

How lipids empty the stomach of birds and mammals slower than other components is still not fully known but the stomach's role in the processing of dietary fats in mammals is well appreciated (Carey et al. 1983). Ingested fats must be emulsified or solubilized in the stomach prior to the formation of micelles in the aqueous contents of the duodenum. Potential emulsifiers that can function in the acid milieu of the stomach include peptic digests of dietary protein, complex polysaccharides, and dietary phospholipids. Some enzymatic hydrolysis of triglycerides is known to occur in the stomach of mammals, resulting in digestion of up to 30% of dietary fats (Carey et al. 1983). The monoglycerides formed during this gastric lipolysis aids the emulsification. If the stomach's capacity to perform this initial emulsification is impaired, by, for example, surgical treatment for ulcers, severe fat malabsorption or steatorrhea results.

Intestinal reflux as determinants of digestive efficiency

In seabirds, very little gastric lipolysis is found (Roby et al. 1986, Place & Roby 1986, Place et al. 1989, Jackson & Place 1990). A possible explanation of how seabirds and birds in general assimilate nonpolar lipids so efficiently is the unique character of the "enterogastric reflex". In fowl, as in mammals, gastric motility is inhibited by intraduodenal injections of 0.1 N HCL, 1600 mOsM solutions of NaCl, corn oil, amino acids or by intraduodenal balloon inflation (Duke & Evanson 1972, Duke et al. 1973). An aspect of this feedback regulatory mechanism peculiar to birds, including seabirds, is the occurrence of one or more intestinal refluxes during the period of gastric motility inhibition (Duke et al. 1973, Duke et al. 1989). In the chick this movement appears to be continuous and regular (Sklan et al. 1978) and observations in the turkey indicate that antiperistalsis includes the duodenum and possibly the upper jejunum, but not more distal segments. Intestinal refluxes occur approximately three times more often in Leach's Storm-petrels than in fowl (Duke et al. 1989) and involve the movement of intestinal contents back to proventriculus.

Sklan et al. (1978), using ^{99m}Tc -diethyl-triamino-pentaacetic acid injected via an indwelling cannula in the hepatic bile duct, followed movement of digesta in the chicken via a Gamma camera. About 40% of the injected isotope refluxed to the gizzard within 2 minutes. Clearance of the isotope from the gizzard took $T_{1/2}$ of 20 minutes. Cholesterol, bile salts and pancreatic enzymes were found in the gizzard at 10-20% of the duodenal concentrations. Thirty percent of the fed triglycerides were found hydrolyzed in the gizzard as compared to 50 to 60% in the duodenum. No lipolysis at pH 3.5 was observed, so the authors argued that the hydrolyzed fatty acids found in the gizzard were of intestinal origin. Proteins were 30 to 50% TCA soluble (i.e. hydrolyzed) in the gizzard reaching almost 70% in the duodenum.

Previous time of passage measurements in turkeys showed that time of passage of digesta through the duodenum was 2 to 3 minutes and through the upper jejunum was 4 to 6 minutes (Sklan et al. 1975). These times of passage are too short to account for the considerable digestion observed by the upper jejunum. However, the shuttling of digesta between gizzard and duodenum increases the time the feed is exposed to digestive enzymes. Clearly, absorption in the upper small intestine is favoured by retrograde movement of a large proportion of the digesta. This retrograde movement of digesta complicates however, the determination of absorption with non-absorbed markers in discrete intestinal segments.

Thus, gastric emptying is closely tied to the receptiveness of the duodenum for additional digesta, and the reflux returns the digesta (both gastric and duodenal) for

further processing in the gizzard. In the process duodenal products like monoglycerides and fatty acids are refluxed to the gizzard along with biliary (bile salts, phospholipids, and triglycerides) and pancreatic products (lipases). Gastric production of lipid emulsifiers is replaced in birds by products of normal intestinal lipolysis which are refluxed to a highly efficient emulsification mill, the gizzard. We believe that intestinal reflux is unique to birds and permits high assimilation efficiencies for such nonpolar lipids as wax esters (Roby et al. 1986, Place & Roby 1986, Jackson & Place 1990).

Chemical reactor theory

Penry & Jumars (1986, 1987) have suggested that the principles of chemical-reactor theory can be used to formulate optimization constraints in a general theory of digestion. Chemical-reactor theory recognizes three ideal reactor types: batch reactors, which are filled with reactants, continuously stirred during the reaction, and then emptied of products after a given reaction period; plug-flow reactors (PFRs), in which reactants continuously enter and products continuously exit with no mixing along the flow path; and continuous-flow, stirred-tank reactors (CSTRs), in which reactants continuously enter and products continuously leave a stirred vessel. Performance equations for these reactors, together with kinetic models for simple enzymatic catalysis and microbially mediated (autocatalytic) digestive fermentation, reveal necessary relationships among initial concentrations of the limiting food component, gut volume, throughput time or gut holding time, and digestive reaction kinetics.

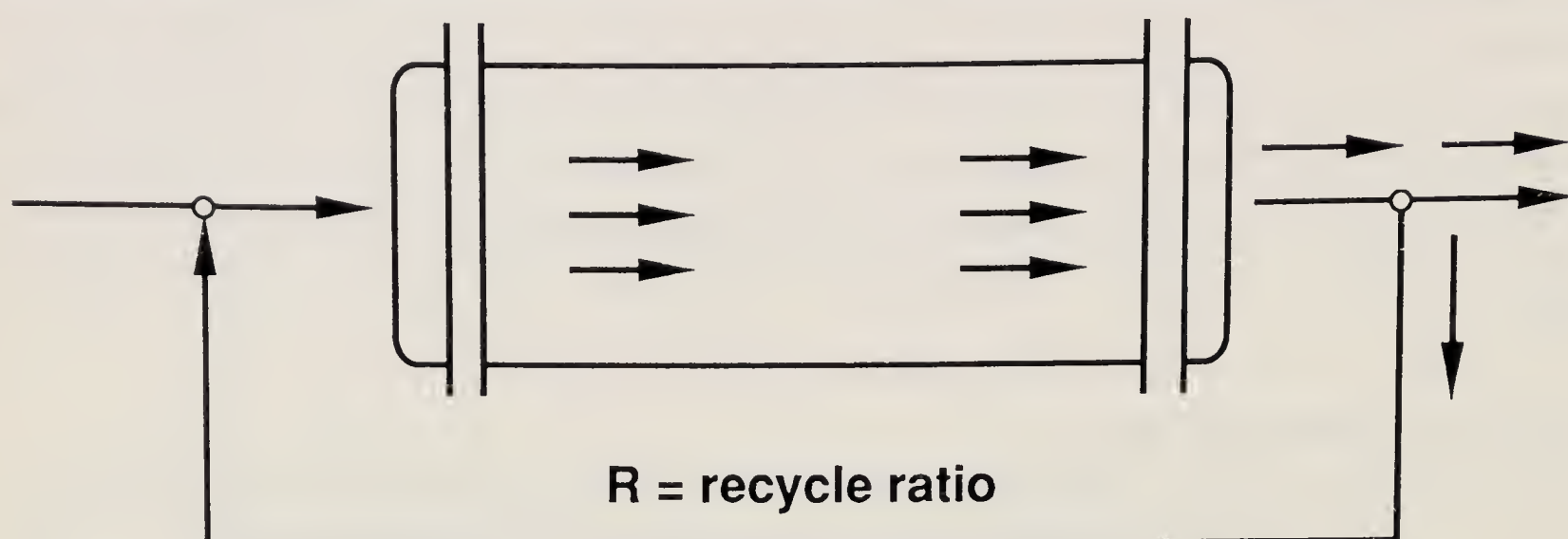
From their analysis, Penry & Jumars (1987) made two general predictions. To sustain the greatest digestive production rate in minima of throughput time and gut volume, an animal dependent on its own digestive enzymes should function as a PFR. Animals fermenting refractory materials should combine a CSTR and a PFR in series at all but the slowest throughput rates, when a PFR will suffice.

A type of chemical reactor extremely important for autocatalytic reactions such as lipid hydrolysis is the recycle reactor in which part of the product stream from a plug flow reactor is returned to the entrance of the reactor. This mode of operation is often applied with autocatalytic reactions, which are self-accelerating, such as many fermentation reactions. Some reaction products are necessary to start the reaction and therefore the feed stream is mixed with a part of the reactor product. The recycle ratio (R) is defined as

R = volume of fluid returned to the reactor entrance/volume leaving the system

This recycle ratio can be made to vary from zero to infinity. Reflection suggests that as the recycle ratio is raised the behaviour shifts from plug flow ($R = 0$) to mixed flow ($R = \infty$). A comparison of the single plug flow with the single mixed reactor finds: (1) for final conversions smaller than the point of maximum rate the mixed reactor is better than any recycle reactor, and (2) for conversions higher than the point of maximum rate the recycle reactor with the proper recycle ratio is superior to either the plug-flow or mixed reactor (Levenspiel 1972). Because of the unique gastrointestinal reflux exhibited by birds, I suggest that birds have adopted a reactor design optimized for minimal volume and high yield - a digestive system that performs like a plug-flow reactor with optimal recycle.

FIGURE 2 - A schematic drawing of an idealized plug-flow reactor with recycle.



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THE AVIAN FEEDING SYSTEM: INTESTINAL NUTRIENT ABSORPTION IN BIRDS

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ABSTRACT. The ultimate goal of the avian feeding system is the transport of nutrients into general circulation for use in metabolic processes. For dietary carbohydrates and proteins, the primary mechanism of absorption involves carrier-mediated transport of simple sugars and amino acids across the intestinal epithelium. A bird's uptake capacity is determined by the number, capacity, and regional distribution of these transporters in its gut. Interspecific comparisons indicate that the integrated uptake capacity (IUC) is genotypically adapted to species' body size and diet. As a group, birds have unremarkable intestines, and comparisons of IUC with rates of energy expenditure suggest that birds may function close to an energetic ceiling imposed by the gut's ability to absorb nutrients. Rates and rhythms of food intake in species as different as growing chickens, nectarivorous hummingbirds, folivorous grouse and geese, and migratory shorebirds may be governed in part by the intestine's capacity to absorb dietary sugars and amino acids.

INTRODUCTION

Research on feeding in birds has most often focused on the early stages of the feeding process, in particular, the location and seizure of food items. Studies have typically emphasized sensory adaptations that enable birds to find food (visual acuity, audition, olfaction), morphological adaptations that facilitate food gathering (bill and locomotory morphology), or behavioral programs that govern decisions regarding when, where, and what birds eat (foraging theory). Yet, these processes merely initiate a chain of events in the avian feeding system that culminates in the digestion (breakdown and absorption) of foods. It is self-evident that the ultimate goal of the avian feeding system is to provide the bird with nutrients that fuel both metabolism (thermogenesis, activity) and production (growth, laying, molt). Yet, comparatively little attention has been given to digestive processes that yield these nutrients. Instead, students of the avian feeding system have usually treated the digestive system as a "black box" and characterized it solely on the basis of measures of gross digestive efficiency. But digestion, like feeding or metabolism, is a rate process; just as rates of food intake and energy expenditures are remarkably high in birds, so must the rate at which nutrients are processed by the digestive system also be remarkable. A bottleneck in the rate at which a bird's digestive system can provide nutrients will impact the individual's fitness as certainly as will a bottleneck in its ability to find or procure food.

Through selective pressures for rapid and efficient feeding, birds have come to devote a disproportionate amount of their tissue mass to sensory, locomotory, and feeding structures, resulting in adaptations that are both elaborate and well-celebrated. In contrast, the alimentary tracts of birds are largely unremarkable. Proportional gut mass is somewhat higher in birds than in mammals (Calder 1984), but most of this difference is attributable to the mass of the crop and gizzard, structures that are ab-

sent in mammals. The avian intestine is actually smaller than its mammalian counterpart, and has less surface area for absorption. The paradox posed by the combination of high metabolic rates and limited surface area for nutrient uptake suggests the possibility that functional (cellular) adaptations of the intestine may be of special importance in birds. In this paper, I review the evidence for adaptive regulation of avian intestinal nutrient uptake and for constraints it may impose upon foraging, metabolism, and production.

NUTRIENT UPTAKE PATHWAYS

Broadly defined, digestion refers to a series of processes by which large and complex molecules ingested as food are first broken down into progressively smaller and simpler subunits, then are absorbed by intestinal enterocytes across the "brush-border" membrane, and finally are moved out of the enterocytes and into the bloodstream for use in metabolic processes. In the steady state, net fluxes averaged over time must be equal through each of these steps. For carbohydrates and proteins, nutrient uptake is facilitated by carrier proteins (transporters) in the brush-border epithelium which move monomers (hexose sugars, amino acids) from the intestinal lumen into the enterocytes. These transporters are typically quite specific to the nutrients they transport: in birds, there are at least two distinct sugar transporters and at least five distinct transporters for the 20 common amino acids that comprise dietary proteins. An individual bird's capacity to absorb nutrients is a function of the numbers, capacities, and distributions of these transporters across its intestine.

Until quite recently, the quantification of intestinal nutrient uptake across the brush-border relied upon *in vitro* techniques that yielded results that were difficult to equate with uptake rates *in vivo* or with nutrient intake (feeding) in living animals. However, the development of the everted sleeve technique (Karasov & Diamond 1983) provided a simple and direct method for estimating uptake of simple sugars and amino acids that are directly comparable to rates in intact organisms. In this technique, segments of intestine are removed from the animal, everted and mounted on glass rods to expose and isolate the brush border. These segments or "everted sleeves" are then incubated in solutions containing a sugar or amino acid of interest, including trace amounts of radiolabeled (^3H or ^{14}C) nutrient. Rates of nutrient uptake in the sleeve are calculated from rates of accumulation of the radiolabeled nutrient in the tissue, as determined by liquid scintillation counting. Uptake rates can be compared between sleeves taken from different gut regions within an individual, for different nutrients in adjacent sleeves, or from sleeves taken from different individuals or different species. Furthermore, uptake rates from sleeves taken from representative regions throughout an individual's gut can be used to calculate an integrated uptake capacity (IUC) for the whole animal by multiplying the length of each gut region (cm/region) times the rate of nutrient uptake per 1-cm sleeve (uptake/cm) and summing these products (uptake/region) across all regions of the gut (uptake/whole gut = IUC).

To date, estimates of IUC for glucose, a representative sugar, and for proline, a representative amino acid, have been published for 11 bird species (Table 1) spanning a wide range in body mass (M_b from 3.2 g to 3,820 g) and diets. These provide a small data base for a preliminary analysis of the effects of body size and diet on uptake capacity, and to determine what adaptations or constraints IUC may provide to the avian feeding system.

REGIONALIZATION OF UPTAKE

In all bird species studied to date, the primary site of nutrient uptake is the small intestine (SI). Within the small intestine, the regionalization of nutrient uptake varies widely with species and with nutrient making generalizations difficult. In most vertebrates, uptake rates of sugars (i.e. glucose) and amino acids (i.e. proline) are highest in either the proximal SI or mid SI and lowest in the distal SI (ileum). Some bird species conform to this pattern, especially those with nutrient-rich diets such as nectar (Rufous Hummingbird *Selasphorus rufus*; Karasov et al. 1986), seeds (Domestic Chicken *Gallus gallus*; Rock Dove *Columba livia*; Obst & Diamond 1989), and meat (Loggerhead Shrike *Lanius ludovicianus*; Karasov et al. 1986). However, uptake in a number of bird species remains relatively constant or actually increases along the length of the SI. These species have comparatively bulky diets such as fruit (American Robin *Turdus migratorius*; European Starling *Sturnus vulgaris*; Gray Catbird *Dumatella carolinensis*; Cedar Waxwing *Bombycilla cedrorum*; Karasov & Levey 1991), foliage (Canada Goose *Branta canadensis*; Obst & Diamond 1991a), or plankton (Red-necked Phalarope *Phalaropus lobatus*; Obst et al. in prep.) and high rates of passage. In mammals, similarly high levels of uptake are induced in the ileum during bouts of hyperphagia, presumably triggered by increased concentrations of nutrients reaching the hindgut. This condition is usually transitory in mammals; high ileal uptake is eventually replaced by an overall increase in intestinal quantity if the hyperphagia is sustained. Maintenance of high rates of ileal uptake in many bird species may represent a key avian adaptation that increases IUC without increasing gut mass.

Appreciable rates of uptake for both sugars and amino acids have been also found outside the small intestine. High levels of uptake may occur in the paired ceca, the level varying with nutrient and with species (Obst & Diamond 1989). In species with very short or "vestigial" ceca (Rock Dove, Red-necked Phalarope), cecal uptake contributes little to the IUC of the bird. In contrast, uptake by the very long ceca of the Sage Grouse *Centrocercus urophasianus* contributes over half of the species' IUC for glucose and a third of the IUC for proline. Low but measurable levels of sugar and amino acid uptake have also been documented in the large intestine (colon) in a number of species (Obst & Diamond 1989); however, the avian colon is typically very short compared with the small intestine and colonic uptake therefore contributes little (< 5%) to the integrated uptake capacity of any bird species studied to date.

ALLOMETRY OF UPTAKE AND METABOLIC RATE

By converting the integrated uptake values (moles/min) for glucose and proline into units of power (joules/second or watts), one can compare the intestine's ability to absorb nutrients with the overall energy demands of the animal. In birds, IUC scales to a somewhat higher allometric power ($M_b^{0.82}$) than does basal metabolic rate (BMR, $M_b^{0.72}$; Lasiewski & Dawson 1967) or field metabolic rate (FMR, $M_b^{0.75}$; Nagy 1987). In the range of body mass between 3.2 g and 3.8 kg, values of IUC predicted by a log-log regression of IUC on M_b fall above the log-log regression for BMR on M_b but below the regression for FMR on M_b . At first glance, this might suggest the surprising conclusion that integrated uptake capacity is sufficient to meet the minimal energy demands but is insufficient to meet the actual energy expenditures of free-living birds. However, IUC probably underestimates the intestine's true absorptive capacity since

it ignores the contributions of uptake pathways for all lipids, certain sugars, and some amino acids. Nevertheless, these comparisons do suggest that uptake capacity in birds is closely matched to their energy expenditures with little or no margin of safety. This impression is reinforced by a comparison of avian IUC with that of mammals. At low body masses (< 100 g), mammals have significantly higher IUCs than do birds, yet their FMRs are significantly lower. Thus, small birds appear to live closer to the energetic ceiling set by their intestinal uptake capacities than do their mammalian counterparts. Whether this condition actually constrains a bird's ability to augment food intake in response to increased energy demands (e.g. during sudden cold stress) is not known. Root (1989) has suggested that the northern range limits of North American passerines in winter are tightly correlated with temperature; metabolic ceilings imposed by the inability to absorb nutrients beyond limit imposed by the IUC may provide a plausible physiological basis for this relationship.

ADAPTATIONS TO DIET

In a number of vertebrate groups, species-specific uptake is genotypically related to diet: amino acid uptake is emphasized in carnivores, while sugar uptake is emphasized in herbivores (Diamond & Buddington 1987). Among birds, absolute levels of glucose uptake vary widely between species whereas proline uptake exhibits less interspecific variation (Karasov & Levey 1991). A useful index to the relative emphasis of amino acid v sugar uptake is the ratio of the IUC for proline to IUC for glucose, or P:G ratio. In birds, there is a general correspondence between the P:G and the natural diet, driven mainly by the variation in glucose uptake. P:G is highest in carnivores, intermediate in herbivores and graminivores, and lowest in the nectarivore (Table 1).

TABLE 1 – Body mass, diet, and integrated uptake capacities for glucose and proline as measured by the everted sleeve technique in eleven bird species.

Species	Body Mass (g)	Diet ^a Type	Glucose Uptake (μmoles/min)	Proline Uptake (μmoles/min)	Proline: Glucose Ratio
Rufous Hummingbird	3.2	N	1.26	0.24	0.2
Gray Catbird	32	F/C	1.26	6.50	5.2
Red-necked Phalarope	34	C	0.05	3.53	71.0
Cedar Waxwing	35	F/C	2.12	6.17	2.9
Wilson's Phalarope	56	C	0.05	4.22	84.4
European Starling	71	F/C	0.60	9.03	15.1
American Robin	79	F/C	1.45	9.67	6.7
Rock Dove	240	G	10.9	26.8	2.5
Sage Grouse	1080	H	95.6	59.3	0.6
Domestic Chicken	2920	G	207.0	252.0	1.2
Canada Goose	3820	H	62.0	134.3	2.2

^aDiet: C = carnivore, F = frugivore, G = graminivore, H = herbivore, N = nectarivore.

Birds are remarkable in their propensity to switch diets with age, season, and local resource availability. Seasonal changes in intestinal morphology with diet quality have been documented in a number of bird species; rapid, phenotypic shifts in uptake capacity would seem a likely means for birds to adapt to changes in diet. Few data are

currently available, and those that exist are contradictory. Obst (in prep.) induced shifts in the IUC of migratory Red-necked Phalaropes over just a few days, including an induction of glucose transport using an artificial diet containing 25% carbohydrate. In contrast, Karasov & Levy (1991) reported that low rates of glucose uptake were maintained in four frugivorous passerine species kept on artificial, high carbohydrate diets. The extent and the speed at which birds are able to adjust their uptake capacities for various nutrients in response to diet certainly warrant further attention.

THE CASE FOR ABSORPTIVE BOTTLENECKS

When food itself is not limiting, can limitations in the uptake capacity of the intestine constrain rates of food intake and metabolic activity in birds? If, as discussed above, birds live close to an energetic ceiling set by IUC, how might this affect their feeding rates, energy expenditure, and production?

Growth

As a group, birds include the fastest growing vertebrates and their high and ballooning energy demands during post-natal development pose a challenge to intestinal function. In *Gallus gallus* (Obst & Diamond 1991b), increases in intestinal mass parallel increases in metabolic demands. However, the ontogenetic pattern of nutrient uptake is more complex. A six-fold increase in glucose IUC occurs in two-week-old chicks, coinciding with the exhaustion of the yolk supply and thermal independence of the chick. A three-fold increase in proline uptake capacity occurs in six-week-old chicks, coinciding with the time of greatest absolute body growth and the onset of postjuvenile molt. Thus, although the growth of the intestine is the primary response to the gradually increasing nutrient demands of the chick, acute challenges imposed by ontogenetic transitions are met by swift (and reversible) adaptive responses in the intestine's uptake capacity. Furthermore, the close match between IUC and energy intake during growth suggests that the intestine's ability to absorb nutrients may limit growth rate in the domestic fowl.

Feeding rates

Three studies suggest that the integrated uptake capacity of adult birds limit rates of food intake. Karasov et al. (1986) found a particularly close correspondence between the IUC of Rufous Hummingbirds and their rates of sugar intake. Rates at which the crop is emptied match rates of glucose uptake measured in vitro, suggesting that the intestine's ability to absorb glucose presents a bottleneck to movement of nectar through the digestive system and, ultimately, to feeding rates. This may account for the intermittent feeding behavior of hummingbirds, which can fill their crops with nectar much more rapidly than they can absorb the glucose ingested. Thus, food intake appears to be constrained by intestinal function in tiny birds, though they have the highest density of glucose transporters known in vertebrates and absorption of glucose is 97-99% complete.

Obst & Diamond (1991a) found a correspondence between uptake capacity and patterns of food intake in two avian folivores. In the Sage Grouse and the Canada Goose, IUC is low, reflecting the lower dependence of herbivores on dietary protein and carbohydrates for energy. Beyond this broad similarity, the differences in uptake between the two herbivores are striking and correspond to different strategies of herbivory. The Sage Grouse has effectively doubled its integrated uptake capacity (and gut mass)

through the evolution of extremely large ceca. The position of the ceca near the end of the digestive tract allows it to slowly "mop" nutrients missed by the intestinal uptake. This uptake strategy is coupled with an ecological strategy in grouse characterized by sedentary habits, low and intermittent food intake, and long retention of digesta. In contrast, geese have negligible cecal uptake; they emphasize intestinal amino acid uptake over sugar uptake, particularly in the ileum, where valuable amino acids are "skimmed" from rapidly passing digesta. Food intake is rapid and continuous, and unlike the heavy-gutted grouse, geese are mobile, tracking high-quality forage in space and time.

Finally, Obst et al. (in prep.) compared nutrient uptake in two congeneric phalaropes that use Mono Lake, California as a migratory "pit-stop". Red-necked Phalaropes migrate in short hops, feed en route, and individuals stay only a few days at Mono Lake. Their intestines are small and light-weight but exhibit high uptake capacities for amino acids. Wilson's Phalaropes *Phalaropus tricolor* stage for weeks at Mono Lake and become hyperphagic as they double their body mass in preparation for a non-stop migration to the southern Andes. Their guts are twice the size of Red-necked Phalaropes and have a correspondingly higher IUC. This difference translates into differences in prey selection: Red-necked Phalaropes specialize on nutritious brine fly larvae at Mono Lake, while Wilson's Phalaropes feed on the more abundant, but less nutritious brine shrimp. In laboratory feeding trials, Red-necked Phalaropes cannot survive on the brine shrimp, their small guts and low IUC providing a bottleneck to digestion of the low-quality prey.

SUMMARY AND OUTLOOK

While the existing data base is still small, it nonetheless provides strong evidence for genotypic adaptation of avian IUC to body size (and hence energy demands) and to broadly defined categories of diet. The potentially important role of phenotypic changes in IUC in meeting changing energy demands and diet within the lifespan of an animal remains largely unexplored. Evidence suggests that birds function close to an energetic ceiling imposed by the IUC, and uptake capacity can influence the rate and rhythm of food intake, diet choice, and even the pace of development; more comparative data are needed to determine how general such digestive limitations may be in birds. Clearly, a full appreciation of the avian feeding system requires an understanding of all the steps involved in the location, acquisition, breakdown, and absorption of food.

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SYMPOSIUM 14

PARENT-OFFSPRING RELATIONSHIPS

Convenrs R. E. RICKLEFS and E. O. MINOT

SYMPOSIUM 14

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INTRODUCTORY REMARKS: PARENT-OFFSPRING RELATIONSHIPS

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ABSTRACT. Parent-offspring relationships encompass a web of interactions including relationships between parents and between offspring. Traditional observational studies of parent-offspring interactions recently have given way to theoretical, experimental, and comparative analyses of constraints on parent-offspring relationships. Many recent studies have also investigated these relationships from the functional perspective of the costs and benefits deriving from different behaviours. Most of these relationships involve access to limited resources and the resolution of conflicts between individuals that are further affected both by asymmetries of age or sex and by environmental conditions. The most successful functional studies have combined careful observation with field experiments that test specific hypotheses. A combination of these two approaches with a developmental perspective opens a promising avenue for future studies.

Keywords: Parental care, parent-offspring relationship, development, provisioning, life history, social behaviour, behavioural asymmetry.

At its most basic level the parent-offspring relationship involves the provisioning of offspring by parents. In this context the evolutionary problems resemble those modelled in foraging theory (Stephens & Krebs 1986). For example, the central place foraging model has been successfully applied to provisioning behaviour of Starlings (Kacelnik 1984). But these models depict a maximisation process for a single individual; they do not incorporate the social interactions or conflicting optimisation criteria that characterise parent-offspring relations.

The factors that make the evolution of social behaviour interesting also make research difficult. Most social behaviour involves a web of asymmetries, unknown histories of previous interaction and uncertain genetic relationships. Study of parent-offspring relationships, particularly in birds, offers unique opportunities to examine some tractable problems in the evolution of social behaviour. The basic requirements of parents and offspring during the breeding cycle have been reasonably well characterised. In many instances the parent-offspring relationship can be observed for an extended period and the survival of offspring and adults followed into successive years. Often the genetic relatedness between individuals will be known with reasonable certainty, or it can be determined by such techniques as DNA fingerprinting (e.g. Burke et al. 1989). Also, asymmetries of age and sex are clearly defined and are expressed in similar form, or at least with limited variation, from one family unit to another.

Parent-offspring relationships preserve much of the basic structure of more complex social relationships. There are at least three participants – offspring, mother and father – each with needs that conflict to some extent with those of the other two. Recent theoretical explorations of parent-offspring relationships have incorporated genetic relationship and asymmetries of age and sex. Trivers' (1974) model of parent-

offspring conflict, and Brown's (1974) and Ricklefs' (1975) models of cooperative breeding, were the first to account for the effects of relatedness and age. The models make several predictions but are too general to be rigorously testable. It has become increasingly common to develop detailed evolutionary models based on the asymmetries and genetic relatedness involved in parent-offspring relationships and to test those models with field data (e.g. Clark & Ydenberg 1990). To some extent all papers in this symposium take this approach.

Boersma examines asymmetry in size between offspring. The usual model (e.g. Lack 1947) has been that hatching asynchrony results in a size difference in young and this asymmetry leads to differential competition for food. However, in the Magellanic Penguin it was the provisioning behaviour of the adults that resulted in differential survival, not direct competition between nest mates. Adults used the asymmetry only to establish a priority for feeding. Thus, the outcome of the interaction fits the traditional model but the mechanism more clearly expresses the influence of parental behaviour, rather than sibling competition; the female parent establishes the initial asymmetry and both parents act upon this asymmetry through differential provisioning.

Hussell establishes the asymmetry between parents as providers and offspring as consumers. He models their interaction as a communication system in which the offspring signal a demand based in part on feeding rate and parents establish a supply based in part on demand. Parental feeding rate has a negative effect on nestling demand and nestling demand has a positive effect on feeding rate. Because the basic model is a closed negative feedback loop it predicts an equilibrium point in the begging of chicks and provisioning of adults. The implication of this is that meaningful knowledge of the dynamics of this system can only be obtained by perturbing the system from the equilibrium. Hussell applies his model to experimental data obtained from Tree Swallows.

Gowaty and Droge examine provisioning of young by parents but focus on the asymmetries of parent and offspring gender. Male and female parents make unequal contributions to broods of Eastern Bluebirds. Moreover, there was an interaction between parental feeding and offspring gender. Males feed daughters more than sons; females do not discriminate between the sexes of their offspring.

The male and female attending a nest may not have an equal genetic relationship to the young they are provisioning when paternity is uncertain or when a male disappears during the breeding cycle and is replaced by another. Robertson explores the consequences of this asymmetry in a study of Tree Swallows in which males were experimentally removed and the behaviour of replacement males was monitored. Replacement males were unlikely to kill the existing offspring if the female was still laying but became less likely to accept or care for offspring as the breeding cycle advanced. Moreover, the females apparently affected the replacement males' acceptance of existing offspring by copulating frequently, even after all eggs were laid.

Four of the five papers in this symposium take an essentially functional approach to parent-offspring relationships. Ball examines some of the mechanisms underlying those relationships, particularly the role of hormones in the regulation of behaviour. Because the reproductive endocrinology of most bird species is quite similar, causal relationships between hormones and behaviour are difficult to establish. In fact, birds

exhibit such a high degree of behavioural plasticity that hormones alone can not be regarded as the determinants of parental behaviour. This point has been made in the past (e.g. Eisner 1960) but we now have the results of many field-endocrinology studies to support this view. In particular, studies involving different patterns of parental care, such as brood parasitic and sex-role reversed species, show that there are some consistent, qualitative differences in hormonal profiles but no direct correspondence between hormone and behaviour. The implication is that endocrinology acts as a coordinator of behaviour but does not represent an inflexible constraint to behaviour.

Each of the papers in this symposium addresses a different asymmetry in the parent-offspring relationship and examines how changes in that asymmetry affect the relationship. Moreover, each paper also identifies the importance of developmental stage to the relationship. Development expresses the changing nature of asymmetry in the relationship between parents and offspring throughout the period of parental care. As the offspring grow older they become less dependent on adults while the probability that they will survive to produce grandchildren increases. It is clear that future studies will need to identify age-specific features of the relationship as part of a dynamic model.

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SEX RATIO CONFLICT AND THE EVOLUTION OF SEX-BIASED PROVISIONING IN BIRDS

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ABSTRACT. Sex-biased feeding in which one parent preferentially feeds opposite-sexed offspring is one form of parental provisioning of offspring. We review the possible forms of sex-biased provisioning. Sex-biased provisioning can be in the form of differential provisioning by sex of parent; different sexes of offspring can be provisioned differentially; or there can be interactions between the gender of parent and the gender of offspring. We note that sex-biased provisioning with interactions can be of a symmetrical or asymmetrical type. We provide a table of species which have been examined for sex-biased provisioning, review data demonstrating sex-biased provisioning in Budgerigars and Eastern Bluebirds, review the existing hypotheses to explain sex-biased provisioning, and present a novel hypothesis of conflict over the sex ratio to explain the evolution of sex-biased provisioning.

Keywords: Sex ratio, sex ratio conflict, provisioning, paternal care, parental care, Eastern Bluebirds, *Sialia sialis*.

INTRODUCTION

Brood size, age of nestlings, seasonality, age and experience of parents, relative genetic paternity and maternity, and confidence of paternity are each known or suspected to affect the provisioning patterns of parent birds to their nestlings and fledglings. In this paper we (1) describe and define possible patterns of sex-biased provisioning; (2) review examples of known patterns; (3) remark on the hypotheses for sex-biased provisioning developed by Stamps (1990), and (4) offer a novel hypothesis - conflict over the sex ratio - to account for the evolution of relative provisioning to sons and daughters.

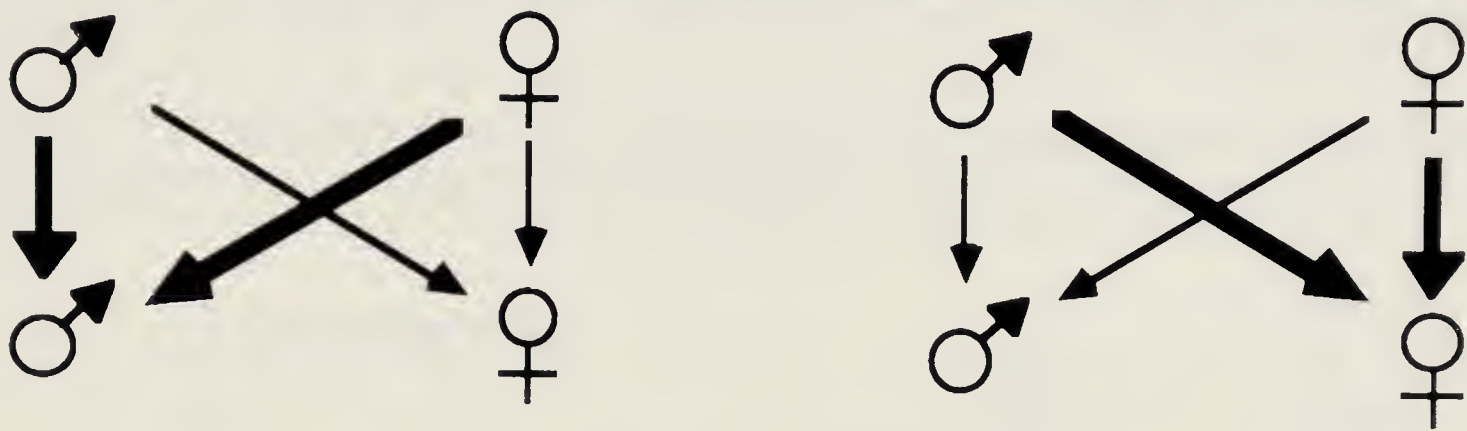
DEFINITIONS

Sex-biased provisioning occurs when offspring of one sex receive more food from a parent than do offspring of the opposite sex (Stamps 1990). In species where both sexes of parents contribute care to offspring, there are three possible patterns of sex-biased provisioning resulting from two sexes of parents feeding two sexes of offspring (Stamps et al. 1987). These include: (1) Provisioning may vary among the sexes of parent with one sex providing more food to offspring than the other (Figure 1A). This is the typical pattern of investment in mammals and in lekking birds where females provide all or most of the provisioning. (2) If one sex of offspring requires more food, due to size dimorphism or other developmental differences between the sexes, both parents may differentially invest in the sex of offspring requiring the most parental care (Figure 1B). Notably, as referenced in Stamps (1990) studies designed to evaluate this idea for birds have yielded mostly negative results i.e. there exists little indication that parent birds actually provision offspring of the larger sex more than offspring of the smaller sex (see below). (3) There may be interactions between parent gender and offspring gender such that one sex of parent differentially invests in one sex of offspring (Figure 1C).

A. Differential Investment by Sex of Parent

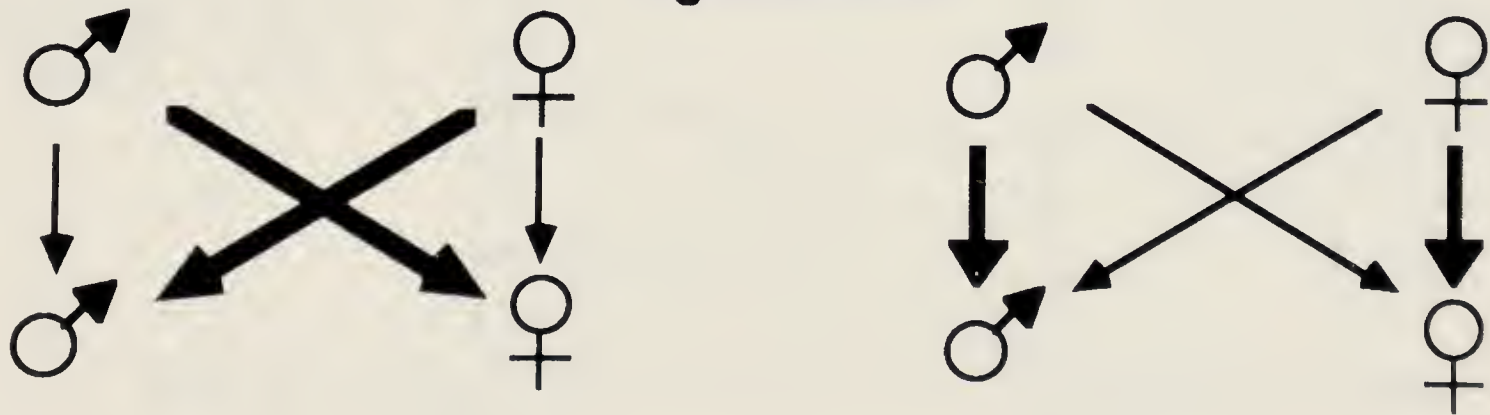


B. Differential Investment by Sex of Offspring



C. Interaction between Gender of Parent and Offspring

1. Symmetric



2. Asymmetric



FIGURE 1 - Diagrammatic representation of three possible patterns of allocation between sex of parent and offspring. The width of the arrows is proportional to the amount of investment.

There are several possible patterns of interaction between the gender of a parent and the gender of the offspring. Complementary or symmetrical gender interactions are indicated by Figure 1C; by “symmetrical” we mean that the only difference between male and female parents is the direction of their provisioning. In symmetrical interactions, if fathers provision daughters, then mothers provide equal provisioning to sons; the contribution of one parent is reciprocal to the contribution of the other parent. Included in symmetrical interactions are those cases where fathers provision sons and mothers provision daughters.

Two other sorts of possible gender interactions are asymmetrical, and non-complementary. In one mothers may provision their sons more than they provision their daughters (Figure 1C), or fathers may provision their daughters more than they provision their sons (Figure 1C). In each of these cases the provisioning of the opposite sexed parent to both daughters and sons is egalitarian, being equally distributed to both sons and daughters.

Other permutations on the patterns in Figure 1 are possible; however, for this paper we will concentrate on the asymmetrical types (Figure 1C2) of parent-offspring inter-

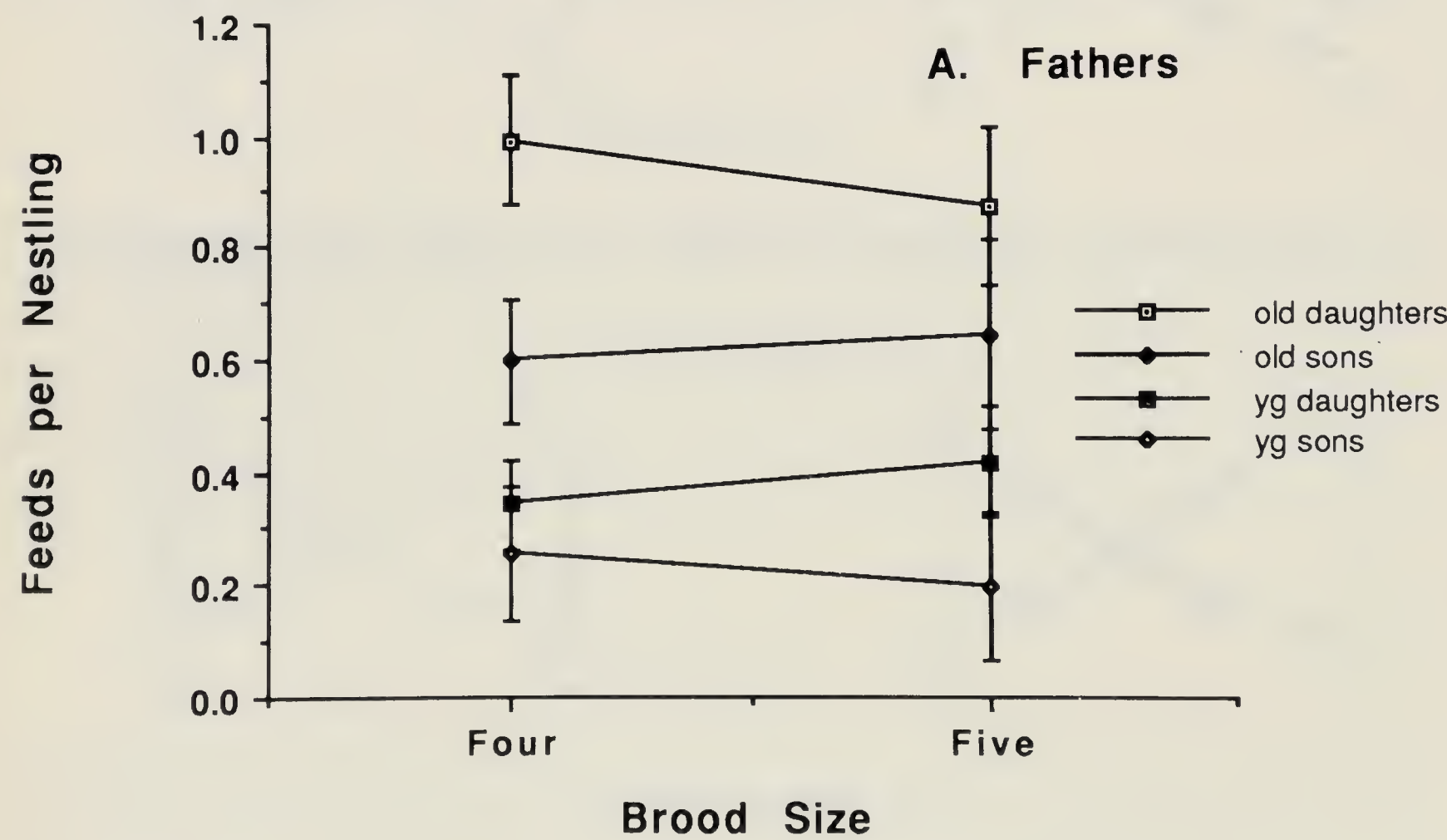
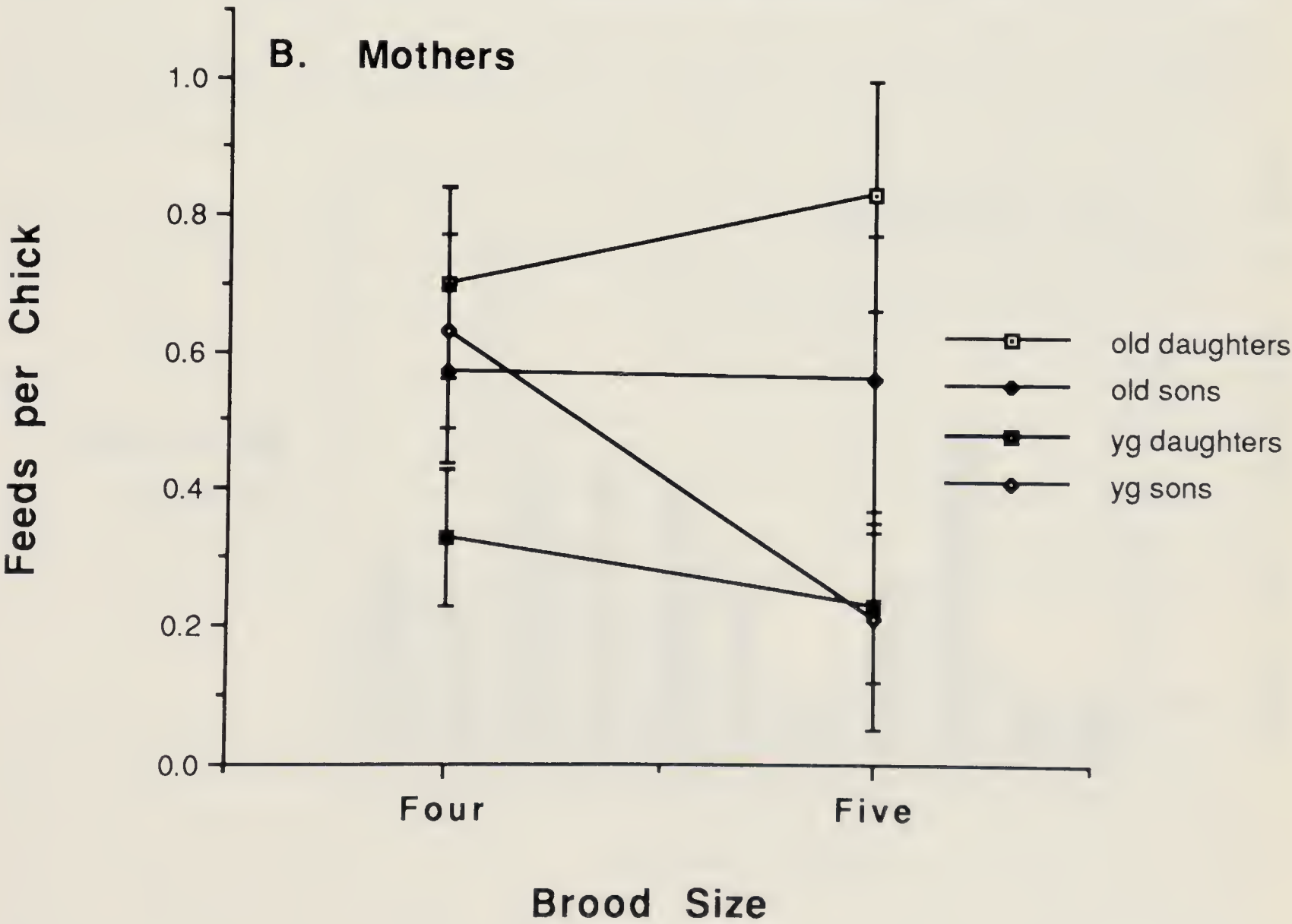


FIGURE 2 - Graph of the number of times male (A) and female (B) care-givers, presumed fathers and mothers, delivered food to broods of Eastern Bluebirds nesting on SC study sites during the field season of 1986. We recorded observations at focal boxes onto check sheets and later transcribed these into computer files. We made all observations in the mornings between dawn and 12 Noon Eastern Standard Time. We observed 90 nests when nestlings were 3 or 4 days old (younger broods) and when nestlings were 9 and 10 days old (older broods). For this analysis we have included only the most frequently observed brood sizes of four and five. During each observation period, each of which lasted for 30 minutes, we recorded the number of times male and female care-givers were on the box looking in without food, the number of times males and females were on the boxes with food, and the number of times either caregiver went into the box with food. We computed feeds per chick by male and female care-givers separately as the sum of the number of times either was on or in the box with food during a given sample divided by the number

action of sex-biased provisioning patterns, because recently a few detailed observational studies (Stamps et al. 1986, Gowaty & Droge in prep.) have led to the speculation that this represents a potentially general pattern of provisioning among birds (Stamps 1990).

EXAMPLES OF SEX-BIASED PROVISIONING

Stamps (1990) recently reviewed provisioning studies. Using references in Stamps (1990) we produced Table 1, which lists provisioning studies in which the relative parental contributions to sons and daughters have been examined. Differential investment by sex of offspring (Figure 1B) is known in some primate and ungulate species (e.g. Clutton-Brock et al. 1981), but we do not know a single clear example in birds. Differential investment by sex of offspring has often been expected in sexually-size dimorphic species (Stamps 1990). We found only one example of clear differential investment to the larger sex in birds (Yasukawa et al. 1990). In this example, both mother and father Red-winged Blackbirds feed their sons marginally but significantly larger amounts of food than their daughters. In Table 1 we also list species that have



of nestlings in the brood. We analysed these data separately for male and female caregivers using PROC GLM (SAS 1985) for a repeated measures analysis of variance with three main effects and their interactions: brood size (4 and 5), age of nestlings (old, young) and sex bias of the brood (“female bias” means that greater than 50 % of nestlings were females; “male bias” that greater than 50% of nestlings were males). For fathers (A) sex bias was significant ($P = 0.03$), as was age ($P = 0.0001$); but none of the interactions were significant. For mothers (B) only age was a significant effect ($P = 0.008$). We graphed the least square means and the least square means standard errors computed from this model.

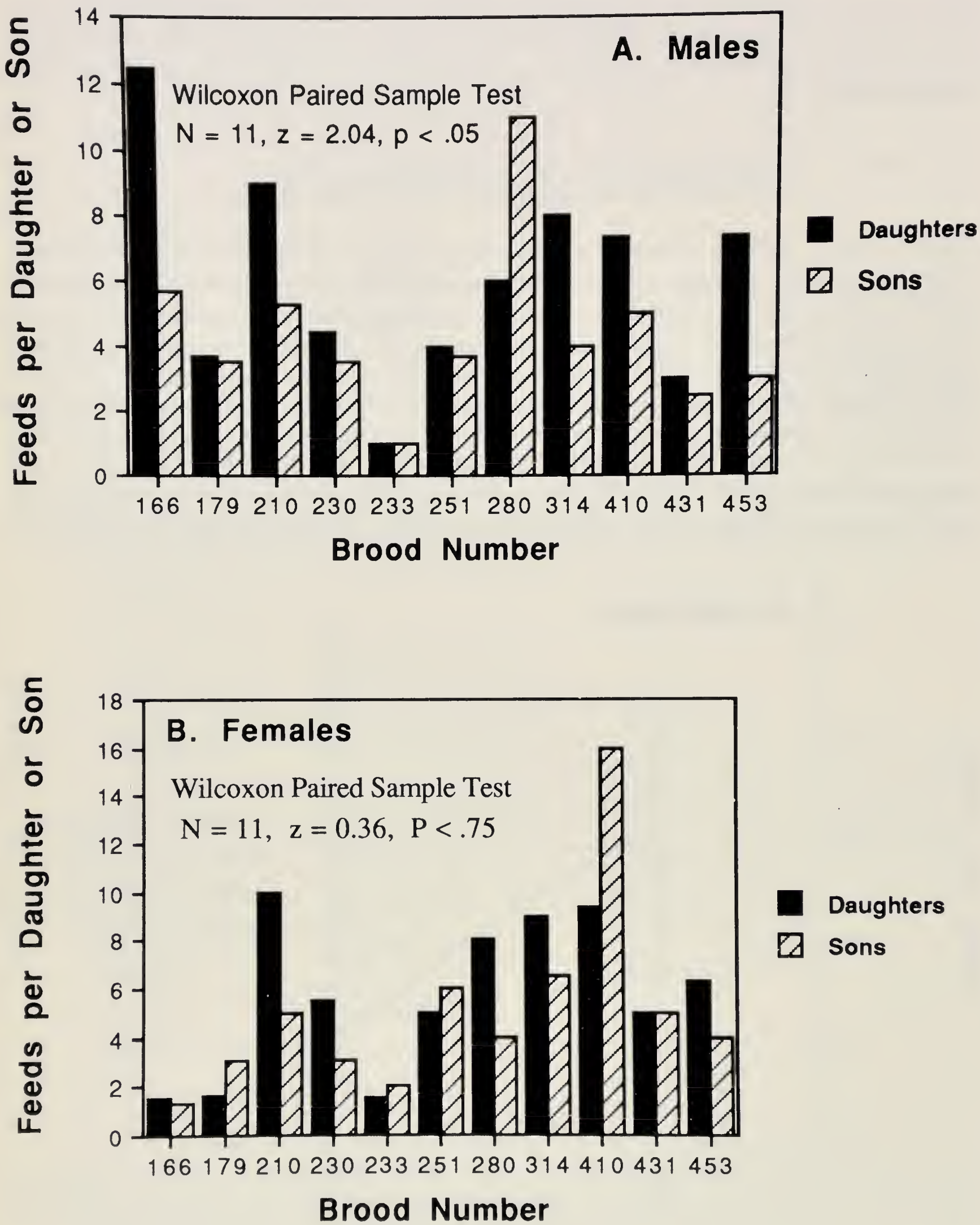


FIGURE 3 - Distribution of feeds per sons and daughters by male (A) and female (B) adults. Each brood is graphed separately (brood number indicates an individual brood). The top graph shows feeds by female care-givers (putative mothers) and the bottom graph shows feeds by male care-givers (putative fathers). We video-taped at least two hours (usually four) at each nest after nestlings achieved asymptotic weight. We made all observations before 1100 hrs. The mean feeds per hour were 5.8 + 3.4 (SD) for males and 5.97 + 2.3 for females. These rates are very similar to observed feeding rates at nests without camera for birds this age (PAG, DLD, pers. obs.).

been examined for evidence of differential investment by offspring sex in birds. For most of the sexually size dimorphic species examined, no differences in provisioning rates to daughters and sons were detectable. In contrast in the two monomorphic species patterns of provisioning reveal an interaction between the gender of the parent and the gender of the offspring (Figure 1C2).

Gender interactions

There are three known examples of interaction in sex-biased provisioning. One is of the symmetrical type (Figure 1C1), in which fathers feed their daughters and mothers feed their sons; two are of the asymmetrical type represented in Figure 1C2, in which fathers feed their daughters more than they feed their sons, but mothers are egalitarian feeders with respect to the sex of their offspring.

ROBINS *ERITHACUS RUBECULA*. Harper (1985) observed a non-significant tendency in a small sample size (N=7) of fledged young for six fledglings to be provisioned by their opposite-sexed parent (Figure 1C1). An interesting correlate of this symmetrical interaction is that fathers tended to feed smaller (based on wing length measures) fledglings (N = 14) and mothers larger fledglings (N=11). Wing length may be a correlate of gender for fledgling Robins as it is for adult Robins (Harper 1985), making the conclusion that father Robins feed daughters and mother Robins feed sons somewhat more interesting. Harper (1985) suggested that fathers "may prefer to rear daughters who are less likely to compete with him" (p. 479), but offered no corollary explanation for the tendency of females to prefer to rear sons.

BUDGERIGARS *MELOPSITTACUS UNDULATUS*. Budgerigars are size-monomorphic, cavity nesting parrots. Observers can distinguish the gender of young Budgerigars by eye colour. In captive domesticated Budgerigars, fathers feed the offspring (on a per offspring basis) in nests with a higher proportion of daughters at higher rates than offspring in nests with more sons (Stamps et al. 1987). In addition, fathers began feeding nestlings in female-biased families earlier than they began feeding male-biased families. However, this effect is directed at entire families: Budgerigar fathers do not selectively feed individual daughters within these daughter-biased broods. Mother Budgerigars are equalitarian feeders with respect to the gender of their nestlings. (Other factors besides gender affect the provisioning patterns of mother Budgerigars: e.g. females selectively feed smaller nestlings.)

EASTERN BLUEBIRDS *SIALIA SIALIS*. Eastern Bluebirds are sexually dichromatic passerines of North America. During the breeding season adult females weigh slightly more than adult males; but males have longer wings and tails than females (PAG, personal observation). Male and female nestlings do not differ at any age in any growth parameters we have measured, including mass, tarsus length, wing length, or tail length (Gowaty 1980, Droge & Gowaty unpub.). Eastern Bluebird fathers feed their daughter-biased broods more than they feed their equal or son-biased broods; mothers are egalitarian with respect to sex bias of the broods. We have observed this effect using two sorts of sampling in two different years.

In the first case, we counted food deliveries to the box by male and female parents. Analysis of variance indicated that sex bias and age had significant effects on deliveries per chick by fathers (Figure 2A); while only age had a significant effect on maternal feeds per chick. In South Carolina the modal brood sizes are five during spring

broods and four during summer broods. Broods of one, two, and three are relatively rare, therefore, we have confined our attention to the effects in broods of four and five.

In the second case, we video-taped inside of nest boxes, so that we could observe directly the gender of nestling to which food deliveries of adult male and female caregivers are directed (Droge & Gowaty in prep.). In matched pairs comparisons, fathers fed their daughters significantly more than they fed their sons (Figure 3A); while mothers did not discriminate among the nestlings on the basis of gender (Figure 3B).

We assign nestlings to gender on the basis of feather coloration when nestlings are at least 12 days old (Pinkowski 1974), about two-thirds of the way through nestling life. Obviously, adult bluebirds may also use this gender signal. However, we suspect that adult bluebirds may be sensitive to gender signals in nestling bluebirds of which we are unaware, because some evidence suggests gender discrimination by parents before primary feathers erupt.

HYPOTHESES EXPLAINING SEX-BIASED PROVISIONING

Sex-biased provisioning may arise because of (1) size differences between sons and daughters, (2) behavioural competition between different sexes of offspring either in the nest, after fledging in family groups, or just after independence, or (3) the greater needs of the dispersive sex in species with sex-biased dispersal (Stamps 1990). However, despite the attention paid to parental provisioning patterns in birds, relatively little is understood about the selective factors, much less the proximate factors associated with provisioning in birds.

Each of the existing hypotheses for sex-biased provisioning arises from differential requirements of the two sexes; whether these requirements are determined by morphological, physiological, behavioural, or demographic considerations distinguishes the hypotheses. "Neediness" in this context refers not only to offspring hunger and energy requirements for growth and independence, but also other variables that affect future reproductive success. This "neediness" approach to understanding the evolution of provisioning is intuitive in that it develops naturally out of considerations of what motivates or controls the behavior of parents towards their dependent offspring. Implicit in these hypotheses is the notion that parents are by and large at the mercy of the selective regimes that render their sons or daughters "needier". For example, this sort of logic would lead one to hypothesize that in species with strong male-male competition for mates and correlated sexual size dimorphism with larger males, parents would be selected to provision their sons more than their daughters. As noted by Stamps (1990) and the references in Table 1, this hypothesis is unlikely to be generally true in birds. Thus, one might question the assumption that parents are selected to respond to the differential "neediness" of their daughters and sons.

There are theoretical reasons as well as empirical reasons for questioning the differential neediness assumption in diploid species: Fisher (1958) was the first to realize that because the reproductive value of sons and daughters is equal in diploid species, parents should be selected to invest equally in their daughters and sons. Fisher's idea is usually applied in discussions about the sex ratio, where the equal reproductive

value of sons and daughters selects for equal numbers of sons and daughters (Figure 4, top). By analogy to discussions of the evolution of the sex ratio, we hypothesize that the reproductive value of sons and daughters selects for equal provisioning by parents to offspring of different sexes (because on average reproductive value of the two sexes is equal).

This sex allocation hypothesis predicts that parents will be selected to differentially provision sons and daughters when the expenditure incurred by daughters and sons differs (Figure 4, bottom). It predicts that when the expenditure incurred of, say, sons is different from daughters for only one sex of parent, while the expenditure incurred by daughters is the same for both parents, gender interaction in parental provisioning should occur. Thus, asymmetric gender interactions may be a reflection of conflict between parents over the sex ratio. We describe how this might occur below. (We use the term "sex allocation" in the sense of Charnov (1982) to mean the relative apportionment of resources to reproduction through male-function and female-function.)

PARENTAL CONFLICT OVER SEX ALLOCATION

If the primary sex ratio (at fertilization) can be modified in birds, it is likely that females have control of the sex ratio in that females are the heterogametic sex. If the secondary (at hatch) sex ratio can be modified, it is likely that females have control over variation in this sex ratio as well, because it is usually only the female that incubates eggs. If the sex ratio at fledging results from the sex ratio at hatch and variation in provisioning patterns from both fathers and mothers, the sex ratio at fledging can be affected by both maternal and paternal contributions. If the optimal sex ratio is the same for both mothers and fathers as Fisher (1958) expected, one might expect no differences in provisioning patterns between the parents. However, if there are different residual reproductive values (through differences in "expenditure incurred" by sex) associated with offspring of different sexes for mothers or fathers, conflict over the sex ratio should exist (Figure 4, middle). Such conflict of interest may be reflected in provisioning patterns to sons and daughters by mothers and fathers (Figure 4, bottom). Conflict in the form of gender interactions in provisioning should be especially obvious in those cases where one sex of parent has little or no opportunity to affect earlier sex ratios.

How can expenditure incurred by a son, say, be less than a daughter for fathers while expenditure incurred by daughters and sons is equal for mothers? The sex ratio of nestlings favours daughters for most passerines (Slagsvold et al. 1986, Gowaty MS). A potential mechanism for this sex ratio variation is local resource competition between the more philopatric sex and their parents (Gowaty MS). By analogy to Clark (1978), which showed that in galagoes adult daughters compete for local resources with their mothers providing selection for son-biased sex ratios, we expect that the philopatric adult offspring (sons in passerines) may compete with their parents, thereby incurring greater expenditure incurred for sons than for daughters, thereby providing selection on sex allocation. If competition with sons is unequal for the parents, being greater, say, for fathers than for mothers, the expenditure incurred by sons will be greater for fathers than for mothers, selecting for conflict over sex allocation in the form of reduced provisionings to sons by fathers relative to father-daughter provisionings and provisionings to both sexes of offspring by mothers. Asymmetric

expenditures incurred through the philopatric sex to parents could be due to increased probability of competition over some resource with the same-sexed parent (e.g. over mates, territories, or food resources). Therefore, we predict that in species with daughter-biased dispersal, in which sons compete with fathers and mothers for nest sites, say, but only with fathers for mates, conflict over the sex ratio in the form of sex-biased provisioning of the form “fathers feed daughters more” will occur.

If passerine fathers have little or no opportunity to affect the sex ratio before the nestling stage of nesting cycles, the “greater expenditure incurred” through sons by fathers should be compensated by their feeding their daughters more than they feed their sons. This leads us to predict that the known examples of asymmetric sex-biased provisioning of the form “fathers feed their daughters more” is the tip of the iceberg; we suspect that this is a general provisioning pattern in passerine birds.

The data on sex-biased provisioning in Eastern Bluebirds seem to fit this pattern. Only mothers incubate; the sex ratio of nestlings favours daughters (Pinkowski 1978, Gowaty 1980 and unpub., Smith, K., pers. comm.) both mothers and fathers feed nestlings and fledglings; daughters disperse (Plissner & Gowaty unpub.); sons are relatively more philopatric and can compete with their fathers for mates. Therefore, the pattern of fathers feeding their daughters more than their sons is consistent with the idea that parental conflict over the sex ratio selects for asymmetric, sex-biased provisioning.

Assumptions of the sex ratio conflict hypothesis

The importance of conflict over the sex ratio to sex-biased provisioning depends on the degree to which the sex ratio lowers the conflicted parent's fitness, relative to the lowering in fitness that equal provisioning already imposed on the conflicted parent. That is, asymmetric interactions in sex-biased provisioning will not evolve if the fitness cost to the conflicted parent of equalitarian provisioning is less than the fitness cost of biased provisioning. That is, the inequality $Db < De$ where Db is the decrement in fitness to the parent from biased provisioning, and De is the decrement in fitness to the parent from egalitarian provisioning, must exist for the evolution of sex-biased provisioning by the conflicted parent.

The “conflict over sex ratio hypothesis” is not concerned with the absolute provisioning to daughters and sons, but with the relative provisioning to one versus the other. It is important to emphasize this distinction because factors that control the absolute numbers of young produced and their absolute requirements for production differ from those that control the relative apportionment of parental resources to son-function or to daughter-function, a distinction noted by Fisher (1958). These considerations expose another important point: relative contributions to sons and daughters are made against the backdrop of constraints on absolute provisioning, as suggested by the requirement that $Db < De$ in order for sex-biased provisioning to occur.

The “conflict over sex ratio” hypothesis is non-intuitive in that it characterizes relative provisioning to sons and daughters not as a source of differential “expenditure” (Fisher 1958) to parents, but as a selective consequence of differential “expenditure” (Figure 4, bottom). We consider the potential validity of this notion below.

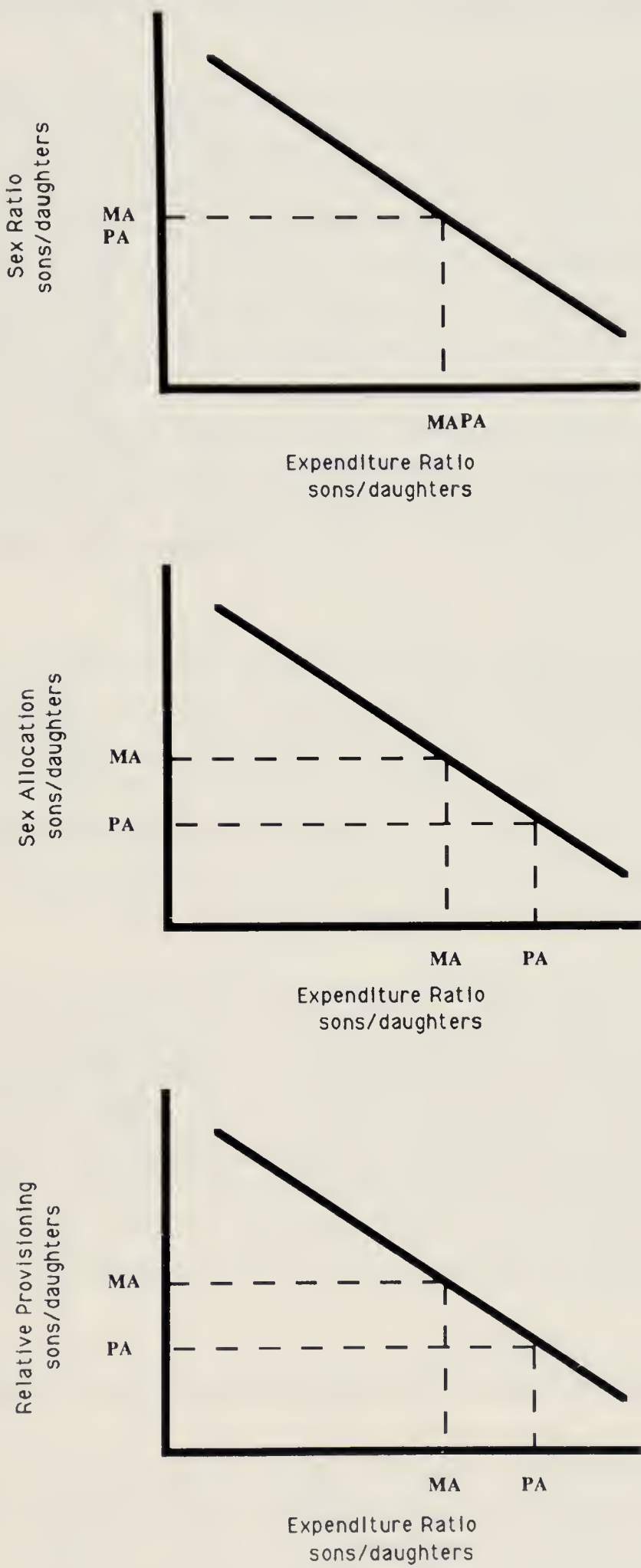


FIGURE 4 - Top: Graphical model of the relationship of the expenditure ratio (incurred in the production of sons and daughters) of mothers and fathers and the sex ratio to sons and daughters. Middle: Graphical model of the relationship of the expenditure ratio of mothers and fathers and sex allocation to sons and daughters, when expenditure ratios for fathers and mothers differ. Bottom: Graphical model of the relationship of the expenditure ratio of mothers and fathers and provisioning ratio to sons and daughters, when expenditure ratios for fathers and mothers differ. The differences in expenditure ratios for fathers and mothers results in conflict between the parents over the optimum sex ratio, reflected here in the optimum provisioning ratios to sons and daughters. In each graph the diagonal line represents Fisher's rule: the number of sons relative to the number of daughters will be inversely proportional to the expenditure incurred on individual sons relative to individual daughters.

IS PROVISIONING A FISHERIAN EXPENDITURE?

It seems to us that relative provisioning is not a Fisherian expenditure for empirical and logical reasons. First, the data are not consistent with provisioning as a Fisherian expenditure. Studies of sex ratio variation in birds have focused primarily on size dimorphic species (Clutton-Brock 1986, Gowaty MS), because researchers believed that size dimorphism between sons and daughters was a good indicator of differential costs of daughters and sons to parents. It was in these species that researchers expected to find sex ratio variation consistent with predictions from sex allocation theory. Yet, few studies of provisioning to sons and daughters have demonstrated differences in the food requirements of daughters and sons to independence. Stamps (1990) noted the relative paucity of evidence for gender biased provisioning in sexually size dimorphic species (Table 1). In fact, the data from size dimorphic species are consistent with the conclusion that sons and daughters incur equal expenditures from the parents.

Relative provisioning might be seen as other than a Fisherian expenditure on logical grounds as well. Modification of the sex ratio can occur through meiotic variations, differential fertilization, selective killing of embryos, or selective killing of dependent offspring. Selective provisioning may be one way that parents can adjust the sex ratio of their offspring. Thus, it does not seem unreasonable to us to think of parental provisioning as a form of Fisherian sex allocation (Charnov 1982), a point on the continuum that results in relative numbers of daughters and sons.

If provisioning itself is not a source of "expenditure" differential to parents, what is? Differential mortality (Fisher 1958), local resource competition (Clark 1978, Gowaty MS), local resource enhancement (Gowaty & Lennartz 1985, Emlen et al. 1987), and local mate competition (Charnov 1982) may provide selection on the relative provisioning to daughters and sons by parents, just as they do on the relative numbers of sons and daughters that parents produce (Charnov 1982). Thought about in this way, provisioning is a part of the continuum of investment decisions that result in the sex ratios we finally observe at the end of the period of parental investment.

DEMOGRAPHIC VARIATION AND CONFLICT OVER THE SEX RATIO

If such logic has generality, it is possible to use these ideas to predict other patterns of sex-biased provisioning. In species with son-biased dispersal, mother adult-daughter competition, and maternal control of the sex ratio through hatching or birth, one would expect son-biased sex ratios (Gowaty unpub.), reflecting that sons, because they leave, incur less expenditures than daughters. Given that mothers are usually in control of the sex ratio to hatch, the expenditure incurred through hatched sons and daughters should be equal for them. However, fathers should be selected to provision daughters more than they provision sons, because the sex ratio that mothers produce reflects a cost of daughters that fathers do not experience. So, hatched daughters should be more valuable to fathers than their relative numbers suggest.

Or, consider a species in which sons, but not daughters, "help" in such a way that the expenditure incurred by them is asymmetric, so that sons incur less expenses for fathers than they do for mothers. This might happen in cooperatively breeding species

TABLE 1 - List of provisioning studies which measured the relative parental contributions to sons and daughters.

Species	Source	Method	Dimorphism	Feeding of offspring
Sparrowhawk <i>Accipiter nisus</i>	Newton (1978)	observation of nests	female larger	food consumption measured by # pieces swallowed equal for male and female nestlings
Common Grackle <i>Quiscalus quiscula</i>	Howe (1979)	ligatures around neck of nestlings	male larger	male and female nestlings received similar quantity & quality of food males (0.124g); females (0.142g)
Red-winged Blackbirds <i>Agelaius phoenicius</i>	Fiala (1981)	manipulated nests to get unisexual broods	male larger	no difference in feeding rates to all- male and all-female broods
	Yasukawa, et al. (1990)	observation of nests	male larger	both male and female make more feeding visits in direct relation to the % sons in the brood
Rook <i>Corvus frugilegus</i>	Roskaft and Slagsvold (1985)	manipulated nests to get unisexual broods	male larger	no difference in male or female feeding to broods of different sex composition
Golden Eagle <i>Aquila chrysaetos</i>	Collopy (1986)	hand reared nestlings and nest observations	female larger	no difference in mean daily consumption rates in captivity or in the wild
Great-tailed Grackle <i>Quiscalus mexicanus</i>	Teather and Weatherhead (1988)	ligatures around nestling's necks	male larger	no difference between male and female nestlings in amounts consumed at any age
Budgerigar <i>Melopsittacus undulatus</i>	Stamps, et al. (1986)	observation	none inside nest box	males fed daughter-biased broods more frequently
Eastern Bluebirds <i>Sialia sialis</i>	Gowaty & Droge, Droge & Gowaty, mss.	feeding visits and observation inside nest box	none	males fed daughter-biased broods more frequently; males fed more feeds/daughters than feeds/son.

in which only males “help”. Assuming that breeding males cannot effect the at-hatch sex ratio, fathers should feed their sons more than they feed their daughters, while mothers should be egalitarian in their provisioning to daughters and sons. A species we would like to examine for such variation is the Red-cockaded Woodpecker *Picoides borealis*, because adult female breeders sometimes disperse from one breeding situation to another (Walters 1990). If breeding competition between mothers and sons can occur, as it might if fathers die or disappear, helpers may help one parent more than the other, so that the potential effects of asymmetric local resource enhancement on provisioning might be observed.

When might mothers’ provisioning not be egalitarian?

We have assumed that mothers have control of the sex ratio up through hatching. When the sex ratio at hatch can be affected by the behavior of both fathers and mothers, so that the hatch sex ratio does not represent the optimum sex allocation for mothers, mothers will be selected to vary their post-hatching provisioning to favor the sex of offspring which incurs less expenditure from them. Therefore, we predict that it will be less likely for non-egalitarian feeding by mothers to evolve in species in which only mothers incubate. Non-egalitarian feeding by mothers should be rare in comparison to non-egalitarian provisioning by fathers in birds. We predict that non-egalitarian feeding by mothers will be more likely in those species in which both fathers and mothers, or in which only fathers, incubate.

CONCLUSIONS

These ideas will remain speculative until we have more information on the interactions between adult-aged offspring and their parents. Are these competitive, cooperative, or neutral? Do they vary as a result of parent and/or offspring sex? Theoretically at least, the Fisherian expenditures associated with conflict over sex ratio are likely to be those factors that can have asymmetric effects e.g. local resource competition or local resource enhancement, rather than differential mortality. We are unable to imagine how differential mortality of daughters or sons could increase or decrease expenditures incurred asymmetrically for mothers versus fathers; while such gender interactions are readily imagined for both local resource competition and local resource enhancement.

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REGULATION OF FOOD PROVISIONING IN BROODS OF ALTRICIAL BIRDS

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ABSTRACT. Regulation of food provisioning involves supply of food to the brood and its allocation among brood members. Food-provisioning behaviour changes as the young develop. To achieve regulation, offspring must communicate their condition by begging, and parents must respond by feeding them. Food availability and other factors influence parental response, but the behavioural system enables parents to compensate for environmental variations. Few studies have quantified the relationships between hunger and begging or between begging and parental response and still fewer have attempted to integrate them into models of the regulation system. Although more observational studies are needed to describe the range of behaviours in altricial birds, the interdependence of food provisioning and begging behaviour limits the usefulness of observations alone for understanding the underlying mechanisms. To elucidate these relationships, observational studies must be combined with experimental tests of behavioural models.

Keywords: Parental care, parent-offspring interactions, food provisioning, begging, altricial birds, regulation, behavioural models, supply and demand.

INTRODUCTION

Altricial birds hatch in a more-or-less helpless state, except for an ability to gape for food, and are fed by their parents (and sometimes by additional helpers) while they are in the nest and usually for some time afterwards (Nice 1962, Ricklefs 1983). Provision of adequate nutrition to broods, in environments that vary in their resources both temporally and spatially, is clearly a problem of great importance to breeding birds. However, regulation of food provisioning is poorly understood.

Birds must allocate their time between foraging and other activities, such as anti-predator behaviour, that contribute to reproductive success. Time apportioned to potentially competing activities may vary depending on availability of food resources. Moreover, when food is scarce and all young cannot be fully provided for, decisions must be made concerning allocation of food among members of a brood. If birds are adapted to take advantage of potential tradeoffs between competing behaviours, we would expect to find mechanisms that enable parent-offspring interactions to be finely tuned to existing conditions.

In this paper I review what is known about regulation, at the proximate level, of the total amount of food provided to broods of altricial birds. I include some examples from species that feed semi-precocial young. In addition, I present results of experiments with Tree Swallows *Tachycineta bicolor* to test a model describing regulation of food provisioning in broods of different sizes. Allocation of food among brood members has important implications for theories of asynchronous hatching, sibling competition and parent-offspring conflict, but I shall not consider it here because of space limitations (see Best 1977, Ryden & Bengtsson 1980, Bengtsson & Ryden 1981, 1983, Hahn 1981, Fujioka 1985, Mock 1985, Khayutin 1985, Stamps et al. 1985, Khayutin et al. 1988).

FOOD PROVISIONING SYSTEM IN ALTRICIAL BIRDS

The food provisioning system in altricial birds can be represented relatively simply (Figure 1). I assume that broods must communicate their condition to parents through "hunger signalling". The response of the parents is likely to be influenced by the availability of food in the environment both directly and through its effects on their own condition, as well as by the hunger signalling of the brood. Feeding reduces begging (the variable component of hunger signalling) both directly and indirectly through changing the nutritional condition of the brood. Other factors might influence food provisioning, such as the phenotypes of the parents or young, but it seems likely that the relationships shown in Figure 1 represent the major influences on the level of food provisioning.

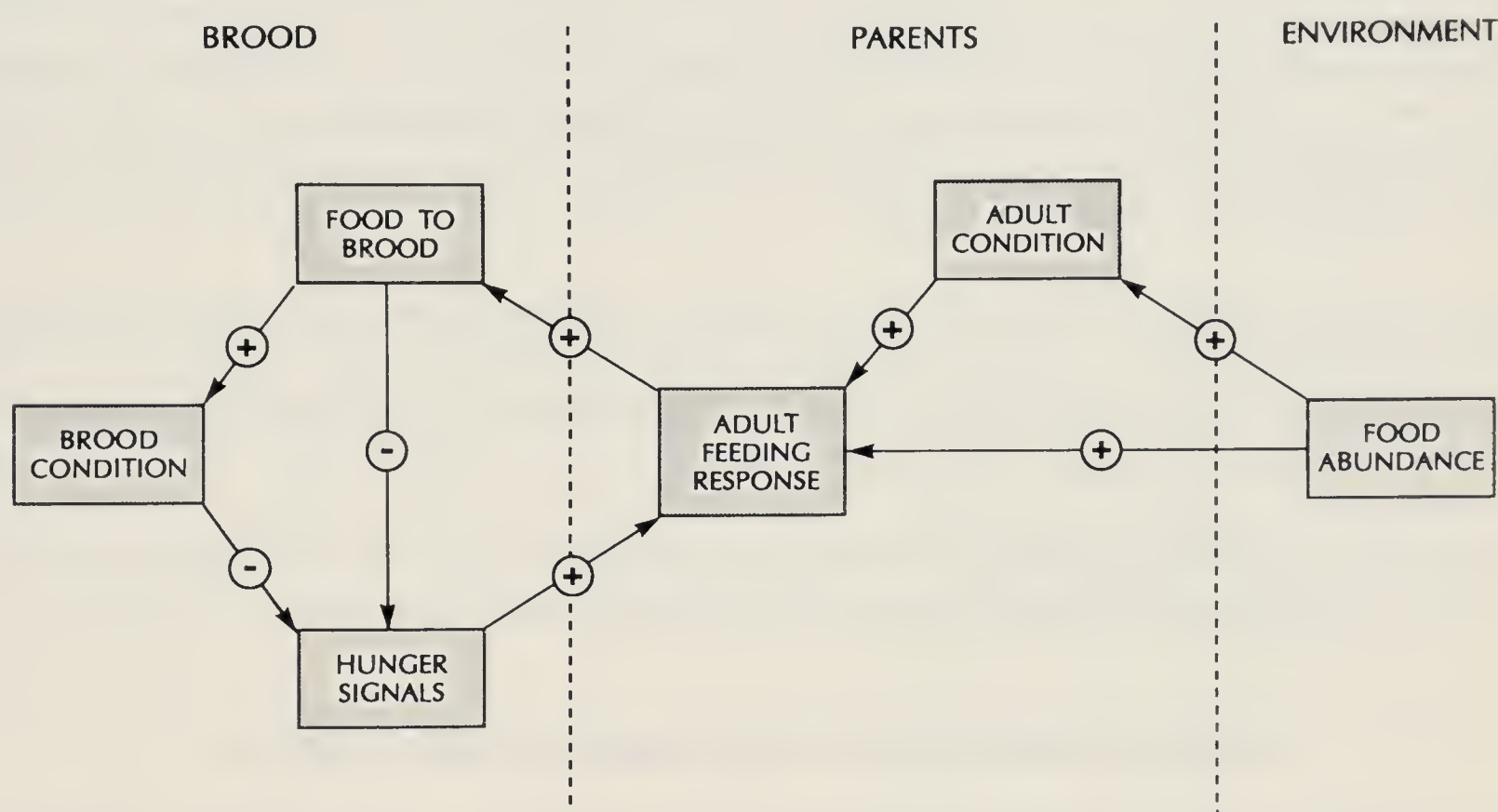


FIGURE 1 - Postulated major components of the food provisioning system of broods of altricial birds. Positive and negative signs indicate the directions of each effect.

If the nutritional requirements of broods did not differ or were relatively predictable, regulation of feeding rate could be achieved by a preprogrammed level of effort by the parents. However, if broods vary unpredictably in their requirements, either between broods (e.g. due to different brood sizes) or temporally within broods, then regulation of feeding rate to an appropriate level can be achieved only if offspring communicate their condition and parents respond. Communication of condition requires that the signal presented by the brood to the adults must be quantitatively related to condition. Moreover regulation of provisioning rate can be achieved only if the response is related quantitatively to the signal, at an appropriate level.

DEVELOPMENT OF FOOD PROVISIONING BEHAVIOUR

In less than three weeks, some altricial young develop from helpless hatchlings that can do little more than gape for food to fully-grown flying birds that feed themselves. The behaviour of the young changes dramatically during this period of growth and development, and we should expect that the mechanisms regulating food provisioning

also change, as illustrated by Khyutin et al.'s (1988) study of the stimuli eliciting begging during each of four major stages in the development of young Pied Flycatchers *Ficedula hypoleuca* (see also von Haartman 1953).

From hatching to the onset of eye-opening (at day 5 or 6), begging of young Pied Flycatchers is elicited by a variety of acoustic stimuli, including feet tapping by the parents on the nest box and the rustle of nest material, or vibration of the nest box. The most important stimulus, however, is the "food call" of the parent. The young also respond to tactile stimuli. The flanges of the bill are particularly sensitive and are often pecked at by the parents if the young do not beg.

From days 5-6 to 8-9, the darkening of the nest box as the parent's body enters becomes the leading factor in eliciting begging. An experiment by von Haartman (1959) indicates that this is not a learned response in Pied Flycatchers. A passive defense reaction (i.e. cessation of vocalization and freezing in response to alarm calls of the parents outside the nest box) develops in this stage. Tactile and acoustic stimuli lose their importance for eliciting begging.

From days 8-9 to day 12, the chicks' passive upward neck-stretching and beak opening are replaced by the chicks turning their heads towards the parent, attacking its bill and snatching away food. This behaviour is triggered by luminosity changes and is directed by the moving silhouette of the adult.

From day 12 to fledging, the darkening of the nestbox loses its importance and the nestlings respond exclusively to the moving silhouette of the adult.

DEMAND BEHAVIOUR – THE STIMULUS FOR FEEDING

Begging behaviour is widespread in birds and it is widely recognized as providing a stimulus to adults to feed the young (Andrew 1956, Barraud 1961, Harper 1986). "Begging" involves various behaviours including directional stretching of the neck, wing shivering, gaping and calling. By repeatedly replacing a brood of two young Pied Flycatchers with two other hungry young, von Haartman (1953) showed that begging behaviour, rather than brood size per se, had a major influence on provisioning rates in different-sized broods. He was also the first to isolate the auditory component of begging as a stimulus evoking a feeding response, by showing that adult Pied Flycatchers responded to the calls of hungry young that they could not see.

If begging behaviour is to function effectively as a stimulus to regulate feeding in a communication system between offspring and parents, it must reflect the nutritional condition of the young. That is, the strength of the begging must indicate hunger level. A positive relationship between begging and short-term hunger level has been stated or implied for several species (von Haartman 1953, Andrew 1956, Barraud 1961, Eisner 1963, Perrins 1965, Bengtsson & Ryden 1981, 1983) but has been reported in quantitative form only infrequently. In Glaucous-winged Gull *Larus glaucescens* chicks, pecks per minute to the parent's bill, calling rate and loudness of calls were all positively correlated with relative degree of food deprivation (Henderson 1975). Black-headed Gull *Larus ridibundus* chicks used different calls depending on whether they were food deprived or satiated, and their calling behaviour was also influenced

by whether they were kept in a cold or warm environment (Impekoven 1971). Food-deprived squabs of the Feral Pigeon *Columba livia* spent more time begging than fed squabs (Mondloch 1989). Calling rates of broods of Tree Swallows *Tachycineta bicolor* were influenced both by feeding rate and by the initial condition of the brood (Hussell 1988).

Visual components of begging clearly direct the feeding response of adults. Successful use of artificial gapes to collect food brought to the young provides experimental confirmation of this for Pied Flycatchers (Betts 1954), Coal Tits *Parus ater* (Betts 1956) and Tree Swallows (McCarty & Winkler 1991). Whether or not visual components of begging influence the response quantitatively, as is required for them to form a part of the food regulation system, remains uncertain. Von Haartman (1953) attempted to demonstrate a quantitative effect on the feeding response of a visual component of hunger signals by placing mirrors on two walls of a nest box occupied by Pied Flycatchers, but feeding frequency did not change. Nevertheless, he thought that the quantitative effects of hunger calls were relatively low and that there must be non-auditory components to the response.

Female Budgerigars *Melopsittacus undulatus* generally preferred to feed the youngest offspring first, often without any prior begging vocalizations from the nestlings, strongly suggesting the importance of visual components of the feeding stimulus (Stamps et al. 1985). Deafened Ring Doves *Streptopelia risoria* did feed their young, although less effectively than those with intact hearing (Nottebohm & Nottebohm 1971), indicating either a non-auditory component to hunger-signalling or a preprogrammed level of feeding, each of which is enhanced by auditory signals.

SUPPLY BEHAVIOUR – THE FEEDING RESPONSE

Evidence for the existence of a stimulus is usually the observation of a response. To achieve regulation of feeding that is appropriate to the size and condition of the brood, the food provisioning response must be modifiable in accordance with the level of hunger-signalling of the young. The well-established tendency in many species for feeding rate to increase with brood size (Moreau 1947, von Haartman 1953, Hussell 1972, and many others) implies a variable response to the needs of the brood but does not indicate the nature of the stimulus. Von Haartman (1953) demonstrated a feeding response by the adults to the hunger calls of the young, rather than to brood size, by showing that visiting rates to a single young Pied Flycatcher increased when the parents could hear the hunger calls of several young in a closed compartment adjacent to the nest box. In Feral Pigeons, begging influenced both the number of regurgitations that the brood received as well as their distribution between the two squabs (Mondlach 1989). Experiments with broods of Tree Swallows confirmed the existence of a supply function, i.e. a positively graded feeding response to increased hunger signalling (Hussell 1988). In contrast, adult Leach's Storm-petrels *Oceanodroma leucorhoa* did not respond to experimentally increased food demand by their chicks (Ricklefs 1987).

Supporting evidence for a parental response to chick hunger comes from demonstration of an increase in feeding in response to playback of recorded hunger calls in Atlantic Puffins *Fratercula arctica* (Harris 1983), Feral Pigeons (Droge 1986), Great

Tits *Parus major* (Khayutin & Dmitrieva 1979, cited in Bengtsson & Ryden 1981, Bengtsson & Ryden 1983), and Zebra Finches *Peophila guttata* (Muller & Smith 1978). A change in provisioning behaviour in response to increased hunger signalling is also implied by observation of increased feeding rates by a single parent when tending a brood alone (von Haartman 1953, Sasvari 1986, Dunn 1989, Whillans & Falls 1990). Deafened Ring Doves did not feed their squabs enough food and abandoned them prematurely (Nottebohm & Nottebohm 1971), possibly indicating a reduction of feeding response with loss of auditory signals. Because the deafening took place at an earlier stage in the reproductive cycle, however, it is not possible to say whether this was a direct effect of an inability to hear the hunger calls of the young or whether it represented a cumulative loss of responsiveness related to previous experience.

It is reasonable to assume that the feeding response of the parents may be modified not only by the begging behaviour of the brood but also by several environmental factors such as food supply and weather as well as by the phenotypes of the parents, which have environmental and genetic components (Hussell 1988). The ornithological literature is replete with examples showing correlations between food supply or weather conditions and feeding rates of the adults or growth rates of young (e.g. Crossner 1977, Murphy 1983, Quinney et al. 1986, Mondlach 1989). There is also evidence from several studies that the response of the adults varies with their age or previous experience (e.g. Klomp 1970, DeSteven 1978, Middleton 1979, Stutchbury & Robertson 1988).

Direct evidence for modification of feeding responses to conditions other than the begging behaviour of the young is scarce. The response of adult Tree Swallows varied both with the hunger signals of the young and the amount of food in the environment (Hussell 1988). In Feral Pigeons, male parents whose foraging costs were high (food mixed with pebbles) did not respond to playback of begging calls while those whose costs were low (food without pebbles) increased their provisioning rates (Droge 1986), indicating a shift in the supply function depending on feeding conditions. The only direct evidence that I am aware of for a change in response depending on previous experience of the adults is in the Pied Flycatcher. When presented with an identical stimulus (a hungry brood of five young), parents that had previously raised a brood of eight fed the nestlings less often than those that had attended a brood of two. Moreover, the parents that had raised a large brood were lighter in weight than those that had raised a small one, indicating that the difference in response of the parents may be related to their condition (Lifjeld 1988). This change in provisioning rate is a clear demonstration of a shift in the supply function (Hussell 1988), which depends on the previous experience of the parents.

REGULATION OF THE FOOD PROVISIONING RATE

Several studies point to the importance of the nestlings' hunger level in the regulation of parental feeding and indicate that the intensity of the broods' begging calls rather than the number of nestlings or other aspects of their behaviour influence the feeding rate (von Haartman 1953, Muller & Smith 1978, Bengtsson & Ryden 1983, Droge 1986, Mondlach 1989, and others cited in the section on "supply behaviour"). Nevertheless, in some species the feeding response seems to be independent of begging rates or nutritional level (Stamps et al. 1985, Ricklefs 1987, 1991).

Von Haartman (1953) argued that the provisioning rate to broods of Pied Flycatchers was controlled by the behaviour of the hungriest nestling in the brood, rather than by the number of begging young. His experiments demonstrated that hunger level rather than number of young is important in regulating feeding rate but, in my opinion, do not isolate the behaviour of the hungriest nestling as controlling feeding rate.

Bengtsson & Ryden (1983) suggested that in Great Tits parental feeding rate is not controlled by the begging of the hungriest nestling but rather by the behaviour of all of the nestlings in a brood, making possible an adjustment of the feeding rate to the average hunger level of the brood. They also pointed out that three main factors could possibly have a role in proximate regulation of parental feeding effort: the working capacity of the parents, the hunger level of the nestlings and environmental conditions such as temperature and food abundance.

Consistent with these conclusions, I was able to show that in Tree Swallows parental feeding of 13-day old broods of six young could be described by two equations, which I called the supply and demand functions (Hussell 1988). The supply function represents the response of parents to the hunger signals of the brood, modified by abundance of food in the environment, and the demand function describes the begging rate of the brood in response to parental feeding rate, modified by the condition of the young. Assuming linear effects, the general forms of these equations are:

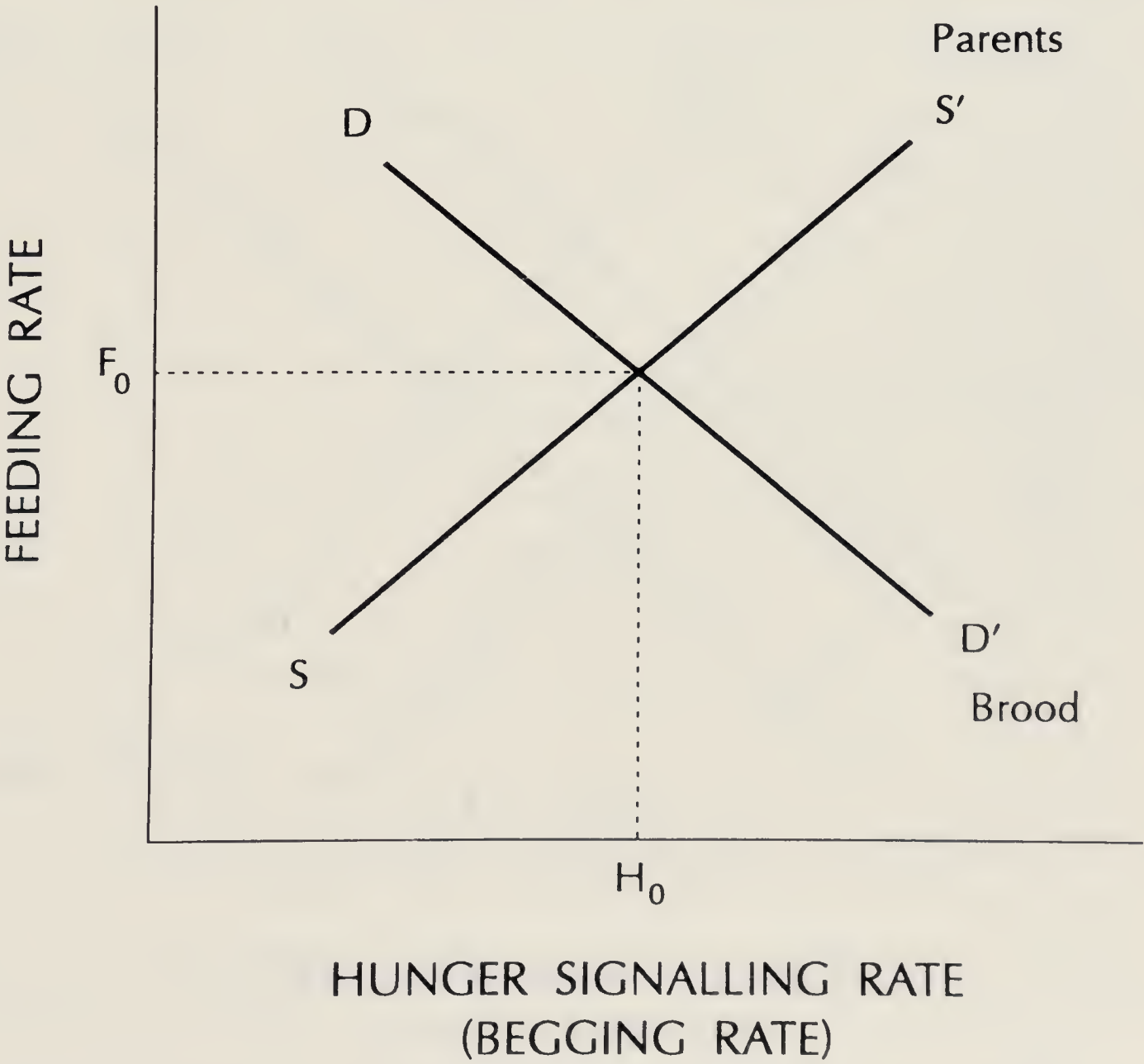


FIGURE 2 - Supply and demand functions of parents and brood, respectively. The demand function D-D' shows the hunger signalling rate of the brood for a given feeding rate. The supply function S-S' shows the feeding rate of the parents in response to the hunger signalling of the brood. F_0 and H_0 are the equilibrium feeding and hunger signalling rates, respectively.

Supply: (feeding rate) = a + b (begging rate) + c (food abundance)

(1)

Demand: (begging rate) = d + e (feeding rate/young) + f (brood condition)

(2)

In equation (1), b and c are positive; and in equation (2), e and f are negative. The solution to these simultaneous equations occurs at the intersection of the supply and demand functions, and represents the begging and feeding rates actually observed in a brood (Figure 2). I provided evidence that the supply function shifts when the food supply changes, in accordance with the third term in equation (1), giving a new solution for begging and feeding rates. Thus a decline in food abundance results in increased begging and a reduced feeding rate (Figure 3) which, if it persists, leads to reduced growth and poorer condition of the young. Also, I showed that, at the same parental feeding rate, broods that are in poor condition (i.e. low in mass) tend to beg more than broods in good condition. That is, there is an upward shift in the demand function as indicated by the third term in equation (2) (Figure 3). This upward shift in the demand function gives a new equilibrium between the supply and demand functions which results in a further increase in the begging rate and an increase in feeding rate. Thus the shift in the demand function enables the brood to communicate its poorer condition to the parents and induces them to compensate for the direct effects of a reduction of food abundance on their feeding response (Figure 3).

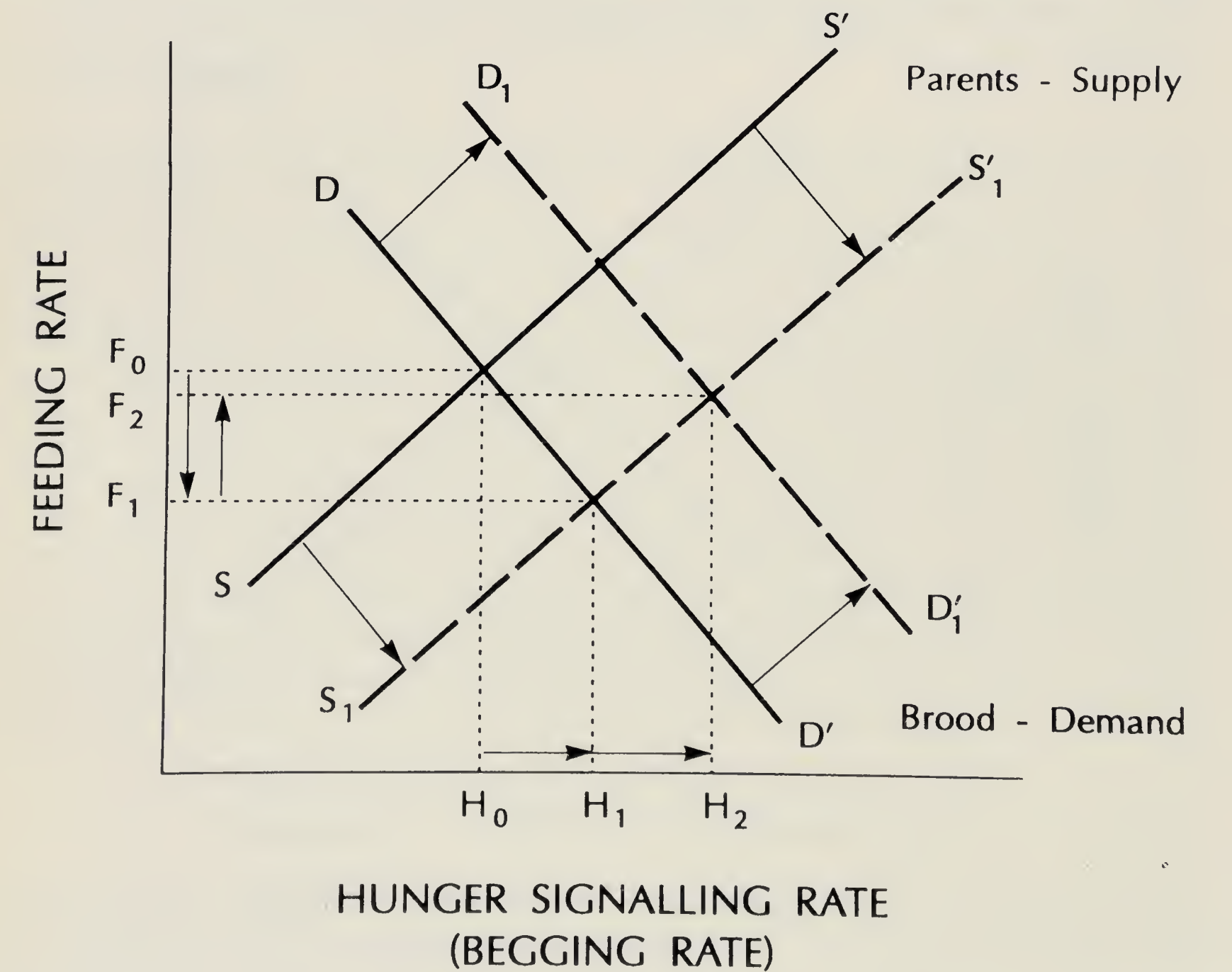


FIGURE 3 - Effects of a downward shift in the supply function (S-S' to S₁-S'₁) followed by a compensating upward shift in the demand function (D-D' to D₁-D'₁). F₀, F₁ and F₂ are the equilibrium feeding rates and H₀, H₁ and H₂ are the corresponding equilibrium hunger signalling rates.

TABLE 1 - Means of feeding rate, hunger-signalling and brood condition variables in 12-day-old broods of 3, 6 and 9 young Tree Swallows.

Variable ^a	Brood Size			p ^b
	3 n=8	6 n=11	9 n=10	
Visits/day	281	354	519	< 0.01
Mass delivery/day (g)	10.2	21.6	32.3	< 0.01
Time calling/day (min)	161	250	437	< 0.01
Calling rate (min per visit)	0.56	0.72	0.86	0.42
Initial Mass (g)	24.4	23.8	22.9	0.26

^a The first 4 variables were measured over a period of 1 day. Initial Mass was measured on the evening prior to the experimental day and was adjusted for age differences among broods (see Hussell 1988).
^b Kruskal-Wallis nonparametric 1-way ANOVA, significance of differences among brood sizes (Sokal & Rolf 1981).

A lesson to be learned from this model is that things are not always what they seem to be. If feeding rates are determined by two variables, as in equation (1), then we must control for each of them to properly estimate the effects of the other. Moreover, begging and feeding rates are interdependent, as indicated by the two equations (1) and (2). This means that the relationships between feeding rate and begging rate in equations (1) and (2) will not be apparent from non-experimental observations in the real world. In my control broods of Tree Swallows, there was no correlation between measures of feeding rate and begging rate in control broods (Hussell 1988: Table 1, Figure 3A), but I was able to demonstrate the existence of supply and demand functions by experimentally transferring broods between nests. In Zebra Finches, the conspicuously marked tongue is moved laterally during the gaping of begging nestlings. Muller & Smith (1978) showed that the rate of tongue movement increased with the age of the nestlings and was slightly but significantly greater during feeding bouts than at other times. However, there was no relationship between the rate of tongue movement and the frequency of feeding of individual nestlings (Muller & Smith 1978: Figure 2), from which they concluded that there was no support for the hypothesis that the parents were stimulated to feed by an increased rate of tongue wagging. If tongue movements and feeding rates are interdependent, as begging and feeding rates are in equations (1) and (2), then increased tongue wagging will stimulate increased feeding by the parents and increased feeding will reduce tongue wagging by the young, so that we cannot predict whether there will be any correlation between the two variables in unmanipulated broods. Under these circumstances, the only way to demonstrate that tongue wagging stimulates feeding is to isolate the variables by conducting experiments. Likewise, Stamps et al. (1985) showed that undersized young Budgerigars were fed more frequently than the largest young and, because size and begging rate were not correlated, they concluded that females fed offspring primarily on the basis of size and did not respond to begging. If begging and feeding rates are interdependent, however, their assumption that begging rates and feeding rates should be positively correlated in unmanipulated broods is incorrect. Again, an experimental approach is needed to show whether or not adults are stimulated to feed by begging. Such experiments have demonstrated that begging stimulates feeding in several other species (see the section on Supply Behaviour).

REGULATION OF FEEDING RATE IN BROODS OF DIFFERENT SIZES

Von Haartman's (1953) study of the Pied Flycatcher started from the observation that large broods are fed more often than small ones and went on to attempt to clarify the mechanism by which this relationship is regulated. He showed that the parents are stimulated to bring food by the begging calls of the young and that the intensity of begging rather than the number of young per se controlled the feeding response of the parents.

In the framework of the supply and demand model, a higher feeding rate in large broods can be explained only if larger broods generate more hunger signals than smaller ones, assuming the parental response curve is the same regardless of brood size (Figure 4). To generate more hunger signals, we would expect the larger broods to be in poorer condition than the smaller ones, unless the extra signals of larger broods derive from their larger number per se or from some interaction between number and condition. That is, the number of young begging or calling at any one time is important rather than the begging behaviour of individual young.

Here I present some results for Tree Swallow broods of three, six and nine young. Data on condition of the young and on feeding, visiting and calling rates were collected from pairs with females at least two years old, in the same way as described elsewhere (Hussell 1988), except that measurements were for 12 day-old instead of

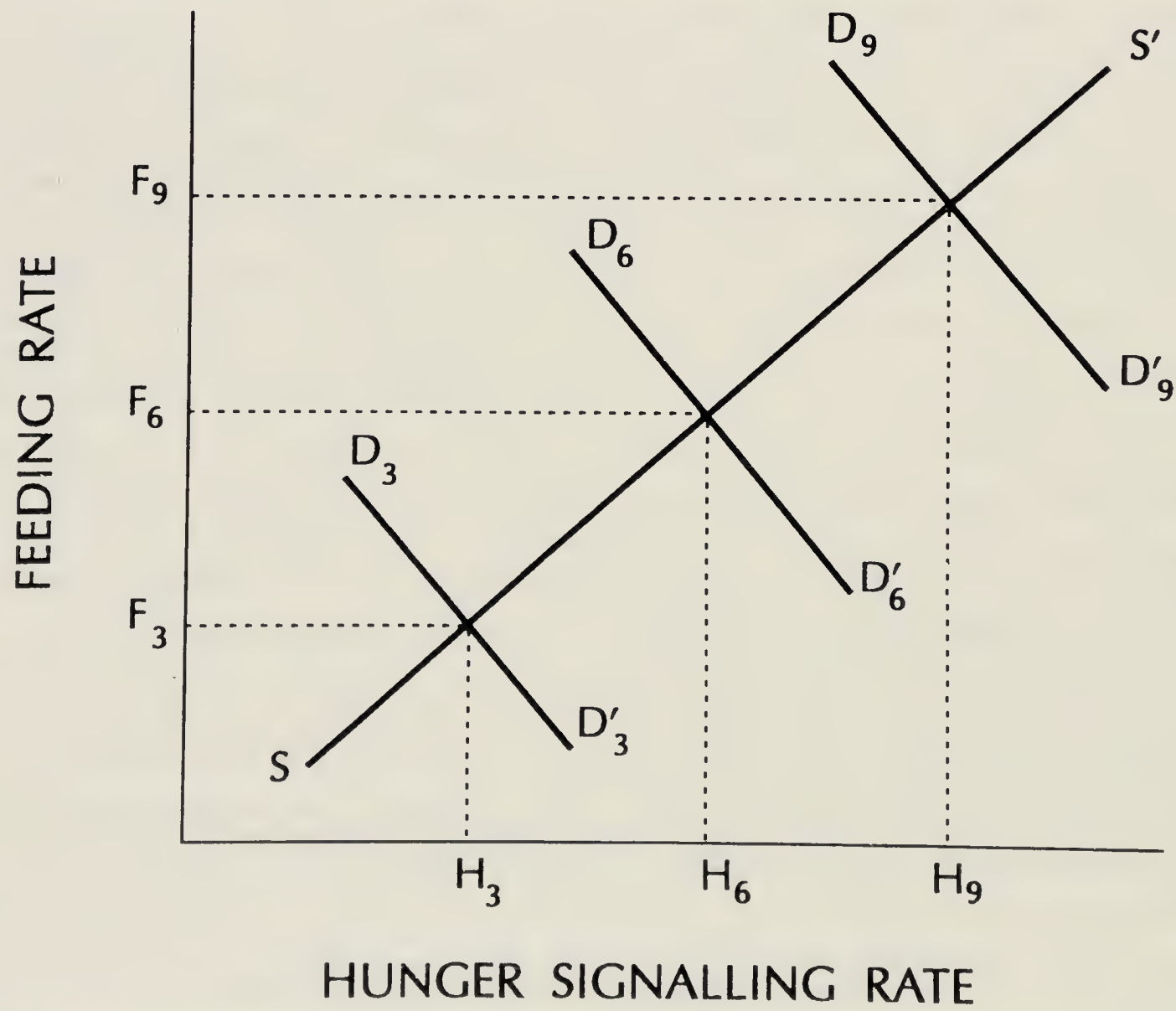


FIGURE 4 - Supply and demand model describing regulation of food provisioning in broods of different sizes. S-S' is the parental supply function. D₃-D'₃, D₆-D'₆, and D₉-D'₉ are demand functions for broods of 3, 6 and 9 young, respectively. F₃, F₆ and F₉ are the equilibrium feeding rates, and H₃, H₆ and H₉ are the equilibrium hunger signalling rates for broods of 3, 6 and 9 young, respectively.

13 day-old broods. Broods of the required sizes were established at the “high-food” site in the 1988-1990 breeding seasons by transferring young among nests early in the nestling periods. Tree Swallow clutch sizes at this site are normally 5-7 eggs, with a mode of six (Hussell & Quinney 1985). Natural broods of three are infrequent and occur mainly as a result of hatching failures. Broods of nine never occur naturally, but artificial broods of nine were often raised successfully.

The average number of visits to the nest each day, food delivered (measured as “Mass Delivery” to the brood, not to individual young, see Hussell 1988) and Time Calling by the brood all increased significantly with brood size (Table 1). Mean Calling Rate (minutes per visit) also increased and the average condition of the brood (measured as mean Initial Mass of individual brood members, see Hussell 1988) decreased with brood size, but differences among brood sizes were not significant.

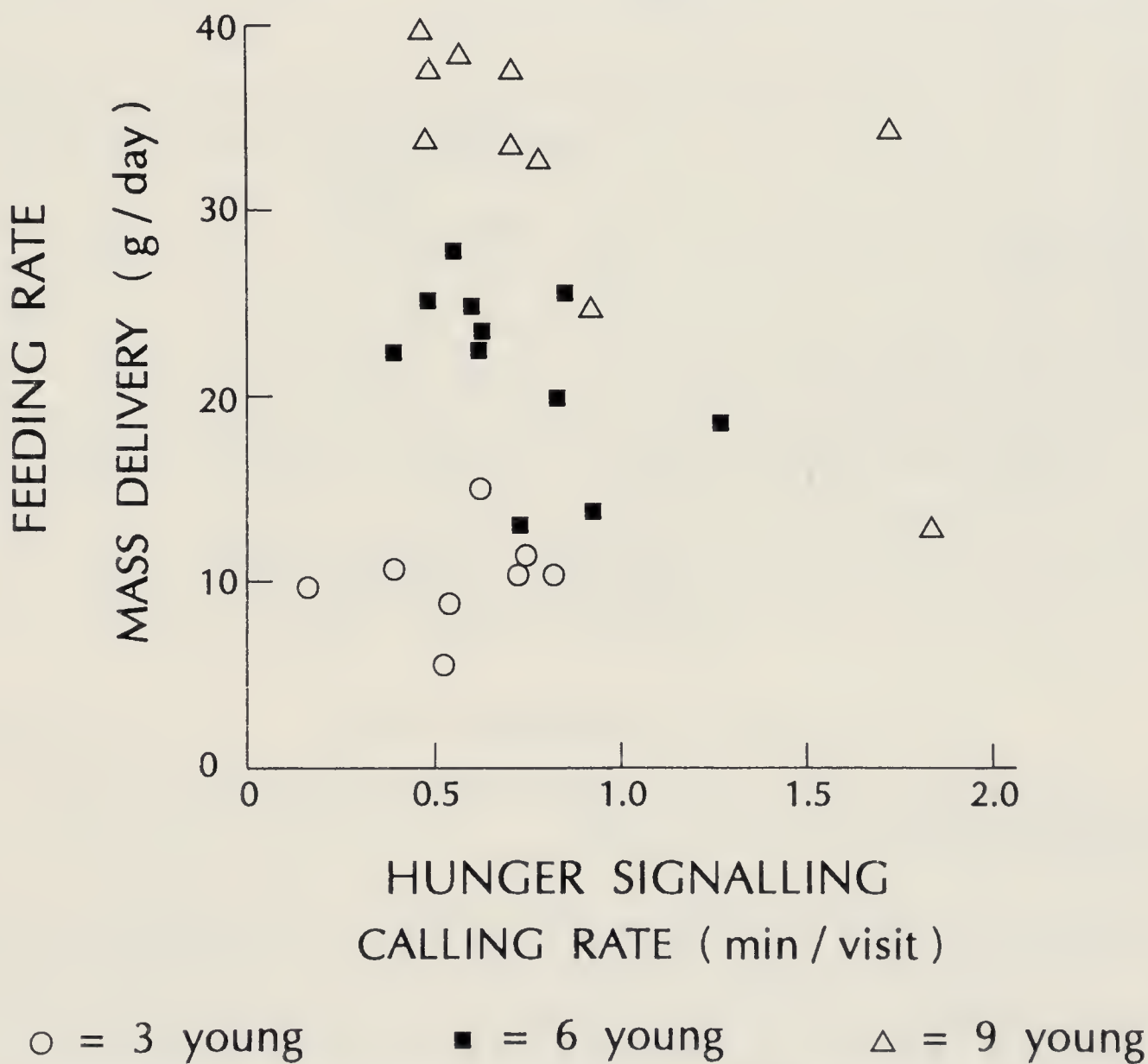


FIGURE 5 - Mass Delivery per day versus Calling Rate in 12-day-old Tree Swallow broods of 3, 6 and 9 young.

Because the young call when the parents visit the nest, the Calling Rate (minutes per visit) is believed to be a better measure of hunger signalling rate than Time Calling. According to the model in Figure 4, both hunger signalling (measured as Calling Rate) and feeding rate should increase strongly and brood condition should decline as brood size increased. Contrary to predictions, feeding rates were uncorrelated with hunger signalling across brood sizes (Table 1, Figure 5; Visits/day v Calling Rate, $r = 0.143$, $P = 0.46$; Mass Delivery v Calling Rate, $r = 0.005$, $P = 0.98$). Calling Rate was negatively related to brood condition, as shown previously for broods of six at 13 days of age (Hussell 1988), but there was no effect of brood size on the relationship (Figure 6; Calling Rate v Initial Mass, $r = -0.628$, $P < 0.01$; ANCOVA, effects of brood size, $P = 0.77$).

Although parents of two broods of nine young performed poorly (Figure 5), average Mass Delivery per young was almost identical and condition of broods was similar regardless of brood size (Table 1, Figure 6). These results suggest that some characteristic of begging or of the brood itself, other than Calling Rate, stimulated the parents to bring more food to large broods and that those signals were not influenced by the condition of individual members of the brood measured as Initial Mass.

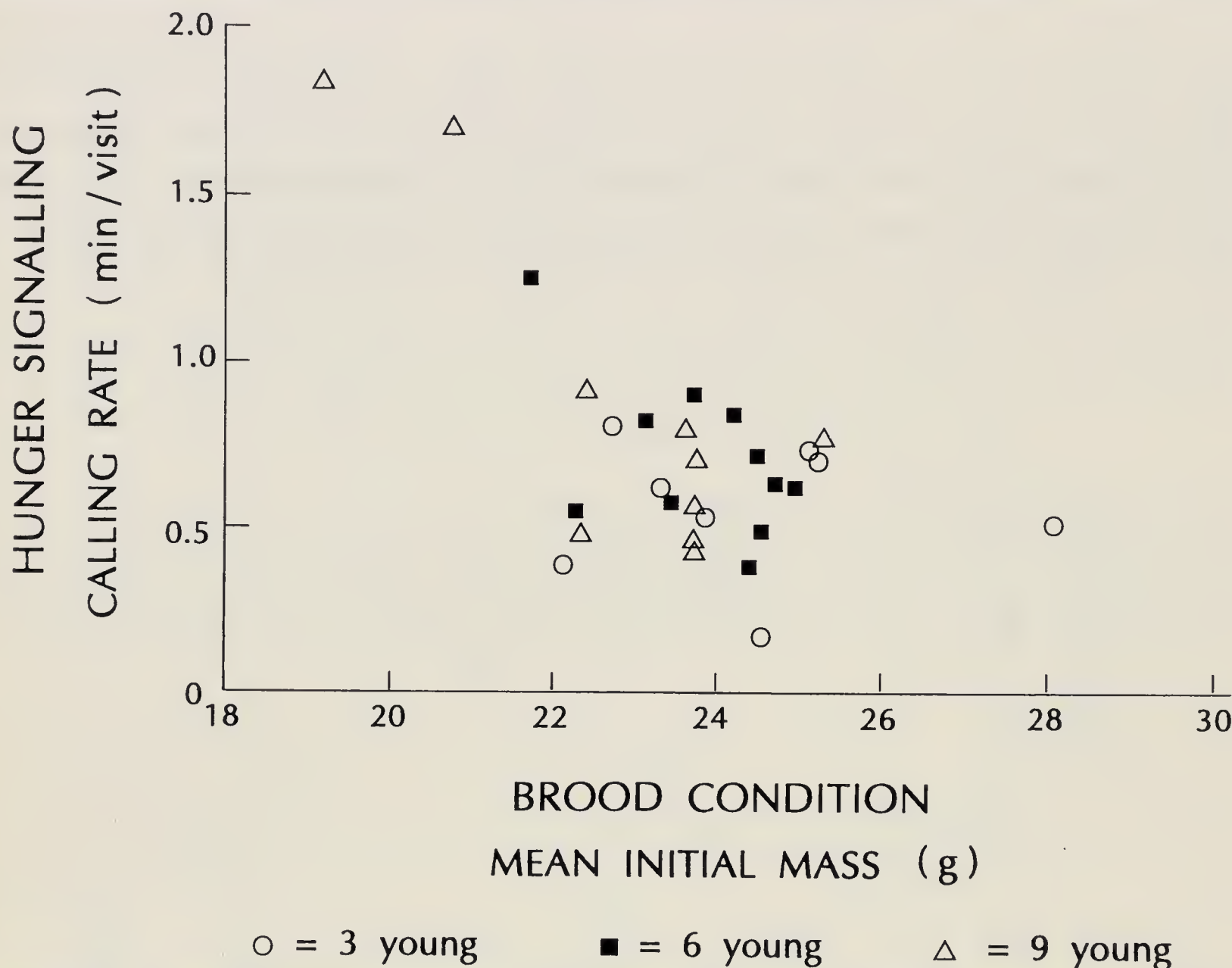


FIGURE 6 - Calling Rate versus mean Initial Mass of individual brood members in 12day-old Tree Swallow broods of 3, 6 and 9 young.

Calling Rate proved to be an adequate measure of (or surrogate for) the variable component of begging that stimulates feeding in broods of six young (Hussell 1988), but it does not appear to represent the differences in hunger signalling that must exist between broods of different sizes. This does not necessarily invalidate equations (1) and (2); it may mean merely that Calling Rate is an incomplete measure of the begging rate of a brood, or that there are other components to hunger signalling.

Equations (1) and (2) can easily be modified to explain the results for different brood sizes of Tree Swallows, by adding a term for brood size in the supply function:

$$\text{Supply: (feeding rate)} = a + b \text{ (begging rate)} + c \text{ (food abundance)} + g \text{ (brood size)} \tag{3}$$

The demand function is unchanged, and g is positive. This change indicates that parents respond to a larger brood by feeding it more, without differences in begging rates among broods of different sizes. This device for explaining the Tree Swallow results is not satisfying, however, because it does not address the mechanism by which a larger brood communicates a demand for more food. It will be an accurate reflection

of how feeding is regulated in broods of different sizes only if parents respond to brood size per se. In view of the evidence that this is not so (von Haartman 1953), we must examine other possibilities.

It seems likely that the number of young gaping or calling during a parental visit may signal the hunger level of the brood, in addition to the length of the calls. If so, we can postulate that begging rate consists of two additive components: calling rate and the number of young begging during a feeding visit. The supply and demand system can then be re-formulated as three simultaneous equations:

Supply: (feeding rate) = a + b (calling rate) + c (number begging) +
d (food abundance) (4)

Demand 1: (calling rate) = e + f (feeding rate/young) + g (brood condition) (5)

Demand 2: (number begging) = h + i (feeding rate/young) +
j (brood condition) + k (brood size) (6)

In these equations, b, c, d and k are positive and f, g, i and j are negative.

These equations can be thought of as a three-dimensional supply and demand model with feeding rate on the vertical axis and calling rate and number begging on the two horizontal axes. The supply surface shifts with food abundance and the demand surface with brood condition and brood size. Nevertheless, we may not need a model as complex as this to explain Tree Swallow behaviour. If calling rate and number begging are strongly positively correlated in broods of one size, calling rate will become redundant and the model will reduce to equations (4) (less calling rate) and (6).

DISCUSSION

The stimuli eliciting a feeding response have been measured quantitatively in a few species: Glaucous-winged Gull, Black-headed Gull, Feral Pigeon, Tree Swallow. Henderson's (1975) approach was most direct. He measured the strength of several behaviours at different levels of food deprivation in Glaucous-winged Gull chicks of different ages. His results illustrate some important points: potential stimuli offered to parents increase with food deprivation, change with age and may involve several different behaviours simultaneously.

Modification of the hunger stimulus by other factors has been rarely demonstrated. Impekoven (1971) showed that vocalizations of Black-headed Gull chicks differed depending on whether they were kept in a cold or warm environment. By testing a model of food provisioning, I inferred that Tree Swallow nestlings, when fed at the same rate, beg more if they are in poor than in good condition (Hussell 1988). This could be tested directly by isolating broods in good and poor condition and feeding them at a constant rate.

A response to begging has been demonstrated in several species, by playback of recorded calls or other experiments: Atlantic Puffin, Feral Pigeon, Tree Swallow, Pied Flycatcher, Great Tit, Zebra Finch. A graded response has been inferred from experiments with Feral Pigeons (Mondlach 1989) and Tree Swallows (Hussell 1988).

Modification of parental response by factors other than begging has been rarely considered or studied. The response was influenced by feeding conditions in Feral Pigeons (Droge 1986) and Tree Swallows (Hussell 1988) and by parental condition in Pied Flycatchers (Lifjeld 1988).

The behavioural system that regulates food provisioning encompasses several interacting variables that can be represented in a simple diagram (Figure 1). Nevertheless, we should expect that models describing this behaviour will be relatively complex in the sense that they will not simply involve single linear relationships between pairs of variables. When variables are interdependent, as is likely to be true of begging and feeding rates, causal relationships cannot be detected by nonexperimental observations. Moreover, because behaviour changes during the nestling period, models and tests of the regulation system should focus initially on particular stages of development.

Although more observational studies of food provisioning are needed to describe the range of behaviours occurring in altricial birds, the interdependence of the food-provisioning response of the parents and begging behaviour of the young limits the usefulness of observations alone for understanding the underlying mechanisms. There is a clear need for more experiments that isolate variables and quantify responses, as well as for development and experimental testing of explicit behavioural models.

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ASYNCHRONOUS HATCHING AND FOOD ALLOCATION IN THE MAGELLANIC PENGUIN *SPHENISCUS MAGELLANICUS*

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ABSTRACT. Magellanic Penguins lay two eggs of equal size four days apart. Differences in incubation results in a hatching asynchrony of two days between the eggs. Nests with hatching asynchrony of 1 to 3 days had higher reproductive success than did nests with synchrony or a larger asynchrony of 4 days. Hatching asynchrony in 2 of the 3 years was significantly correlated with the nest relief interval. Two-day asynchrony maximized the survival of both first and second chicks by increasing the chance that they were fed soon after hatching. Food was limited as evidenced by differences in the average growth of one chick versus siblings. Several pieces of evidence suggest that parental preference and not sibling competition is important in determining the outcome of which chick survives. Adults prefer to feed the larger chick and chicks cannot overcome adults' preference. If chicks could control food allocations, reversals should be more common when chicks are more mobile versus less mobile and younger. Reversals are always rare but are less common when chicks are older. Lastly, there is no evidence that chicks intimidate each other. These facts suggest that adult preferences are more important than sibling competition in determining which chick survives. Facultative brood reduction occurred because adult behavior favored larger chicks, not because of hatching asynchrony.

INTRODUCTION

Most species of penguins lay two eggs from which they rear one or two chicks. Eggs hatch asynchronously and, depending on the species, one or two young are reared (Warham 1963, 1971, 1975, Williams 1980, Van Heezik & Davis 1990, Lamey 1990). For some species, the two egg clutch appears to be an insurance policy against the loss of one of the eggs because only one chick is reared (Williams 1980, 1981). The Magellanic Penguin lays two eggs of equal size; both chicks sometimes fledge but more frequently only one chick fledges (Boersma et al. 1990). Eggs are hatched asynchronously, which creates size hierarchies which promote brood reduction through the elimination of smaller chicks during times of food stress (Lack 1954, 1968, Ricklefs 1965). Thus, asynchrony may indirectly adjust the clutch size to what the pair can rear based upon their foraging abilities and the variable food conditions they experience.

In situations where food resources are inadequate to fledge all chicks, chick survival could be determined either by competition among chicks or by the behavior of adults with respect to which chick is fed. Unless the oldest chick is malformed or unhealthy, the genetic interests of the parent and the eldest chick in who survives are effectively identical. Such overlapping interests complicate efforts to untangle the role of the adults and chicks in chick survival. Passive mechanisms that may set up predictable outcomes of how broods are reduced in the face of food shortages include size and age hierarchies which may arise because of asynchronous hatching. Nevertheless, parents or chicks, through their behaviors, may be able to alter the "predictable" outcome. Since diploid parents are related to themselves 100% and to their offspring by only 50%, selection should favor adults' control in food allocation compared to chicks' control. Thus, adults should secure their own needs first, then their chick's.

Ricklefs' (1969) model hypothesizes that growth rates for young are maximized throughout the nestling period. Obviously, competition among siblings (Ricklefs 1969, O'Conner 1977, 1978) should retard growth of all or at least some siblings since energy must be spent on gaining or denying access to the food. In the most extreme cases, one sibling may kill another (Stinson 1979, Mock 1984, Ploger & Mock 1987). If parents can divide the food equitably among the young, sibling competition may be reduced but energy may be used inefficiently since there may not be enough food to rear all chicks to fledging. Food that goes to a chick that will not fledge reduces the food available for the other nestlings causing them to grow more slowly, fledge later, or die. Likewise, when a sibling monopolizes more food than is essential for its growth and survival, reproductive success of those pairs should be lower than that of pairs that can divide food more equitably. Sibling competition that results in one chick being fed more than it needs and lowering the survival of its nest mates or adult feeding preferences that compromise the survival of the largest chick will lower reproductive success and thereby reduce their parents' fitness. Thus, either too inequitable a division of food or too equitable a division of food when there is not enough to rear all chicks should lead to lower reproductive success and lower adult fitness. When food is limited, parents should minimize energy loss to sibling competition and not rear additional young at the expense of the growth and survival of the nestling that has the highest potential fitness, the largest chick. Presumably there are trade-offs on how much energy can be diverted from first to second nestlings before reducing the overall fitness of the brood. Energy should be invested in the second chick only as long as the fitness of rearing the second chick increases the adults' total fitness. When two chicks, instead of one, are fledged, risks from unpredictable events are spread over two individuals; thus, selection should favor rearing two chicks over one when the pair's fitness if it rears two chicks is equal to its fitness if it rears one. The timing of these trade-off "choices" will depend on the "quality" of the pair (i.e. their foraging ability, general health) and environmental conditions.

Two mechanisms that may facilitate these "choices" are age and size difference among the young. Parental preferences or sibling competition may favor the eldest or largest chick. Asynchronous hatching should improve survival of the first hatched chick over later hatchlings since first chicks are older and generally larger and, therefore, better competitors for food. The death of the youngest chick in times of food stress should promote more efficient use of food and enhance reproductive success.

In this paper, I will try to untangle the complex relationships among parental and chick behavior by examining the reproductive success of Magellanic Penguins. I offer an alternative hypothesis of the role of hatching asynchrony: it is a mechanism to maximize the chance that both chicks are fed soon after hatching and thereby increase chick longevity. I also examine evidence on whether parents divide food equally between siblings and the importance of sibling competition in food allocation.

METHODS

This study is based on 3 seasons of field work (September 1985 to March 1988) at Punta Tombo, Argentina (44° 02' S, 65° 11' W), the site of the largest continental colony of Magellanic Penguins. The September to March field seasons are referred to by the year in which they begin: 1985, 1986 and 1987. Approximately 1500 nests were marked in 10 areas and followed each year from the time the adults arrived in

September until the chicks fledged in February (see Boersma et al. 1990). One study area of approximately 150 marked nests was checked daily, and these data make up the bulk of the data used in the analysis. I restricted the sample and used only eggs and chicks where the date of laying and hatching was known (within one day). Upon hatching, the chicks were removed from their nest, weighed and measured (see Boersma 1974).

In a subsample of nests, chicks were weighed daily and measured every 10 days from hatching until they died, disappeared, or fledged to determine when they were fed and how much weight they gained.

In late January and early February, the time when chicks begin fledging and are most likely to compete directly with each other for food, I watched adults feed chicks. Adults commonly return to the colony late in the afternoon and early evening. I followed adults to their nests and watched while they fed young. When the adult began feeding the chick or chicks until it quit was a feeding bout. Usually the chicks continued to beg long after the adult quit feeding but, in most cases, feeding bouts lasted from 30 minutes to two hours. During the feeding bout, the side to which the adult fed the chick (right or left) and whether the large or small chick was fed (a feed) was recorded. I watched other feeding bouts to gain a qualitative impression of food division between chicks.

Statistical analysis of data was conducted with S (Becker & Chambers 1984) and SPSS. To consider the effects on growth, only nests that had both siblings alive at the time of the visit were used, hence sample sizes vary.

RESULTS

Hatching asynchrony and nest relief

Magellanic Penguins lay two eggs of equal size normally 4 days apart ($SE = 0.04$) which hatch 2 days apart ($SE = 0.06$). Reduction in the interval between the laying of the eggs and their hatching (Figure 1) is caused by the adults' failure to incubate the first egg tightly until the second one is laid. First eggs and second eggs are equally likely to be lost, suggesting that the laying order and interval between eggs has little effect on their survival ($\chi^2 = 0.88$, $n = 189$, $P = 0.50$).

The male usually attended the first egg while the female departed before laying the second egg. Two long incubation bouts, the first by the female and the second by the male, of 15 and 17 days were followed by two short bouts of 4 days (Boersma et al. 1990). Near hatching, incubation bouts shortened to 2 days ($x = 50$ h, $SE = 2$ h, $n = 410$). Hatching asynchrony is closely correlated with nest relief. In 1985, the time a bird remained at the nest during a 13 day period, 6 days before the first egg hatched until 7 days after it hatched, averaged 52 hours ($SE = 4$, $n = 178$). In 1986, during this same 13 day period, birds exchanged duties every 40 hrs. ($SE = 3$, $n = 115$) and in 1987, every 56 hrs. ($SE = 4$, $n = 117$). Hatching asynchrony for these same nests in 1987 was 39 hrs. ($SE = 5$, $n = 20$), in 1986, 45 hrs ($SE = 5$, $n = 15$), and in 1985, 53 hours. ($SE = 5$, $n = 29$). Hatching asynchrony was significantly correlated with the average time between nest reliefs for this 13 day period in 1987 and 1986 (Spearman rank '87 = 0.44, $n = 20$, $P = 0.05$; '86 = 0.70, $n = 15$, $P = 0.009$) but not in 1985 (Spearman rank = 0.05, $n = 29$, $P = 0.8$). In 1987 the number of nest reliefs for the

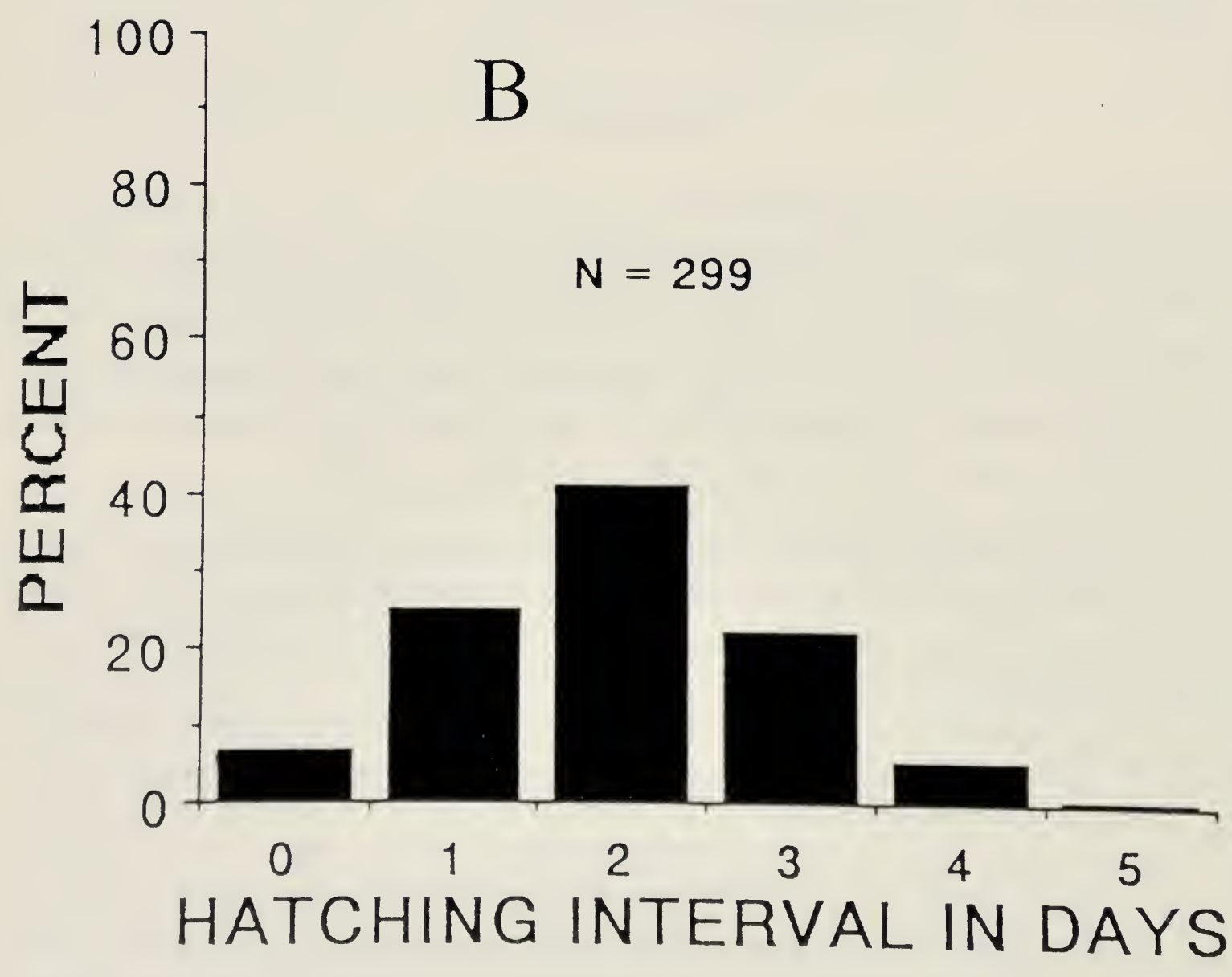
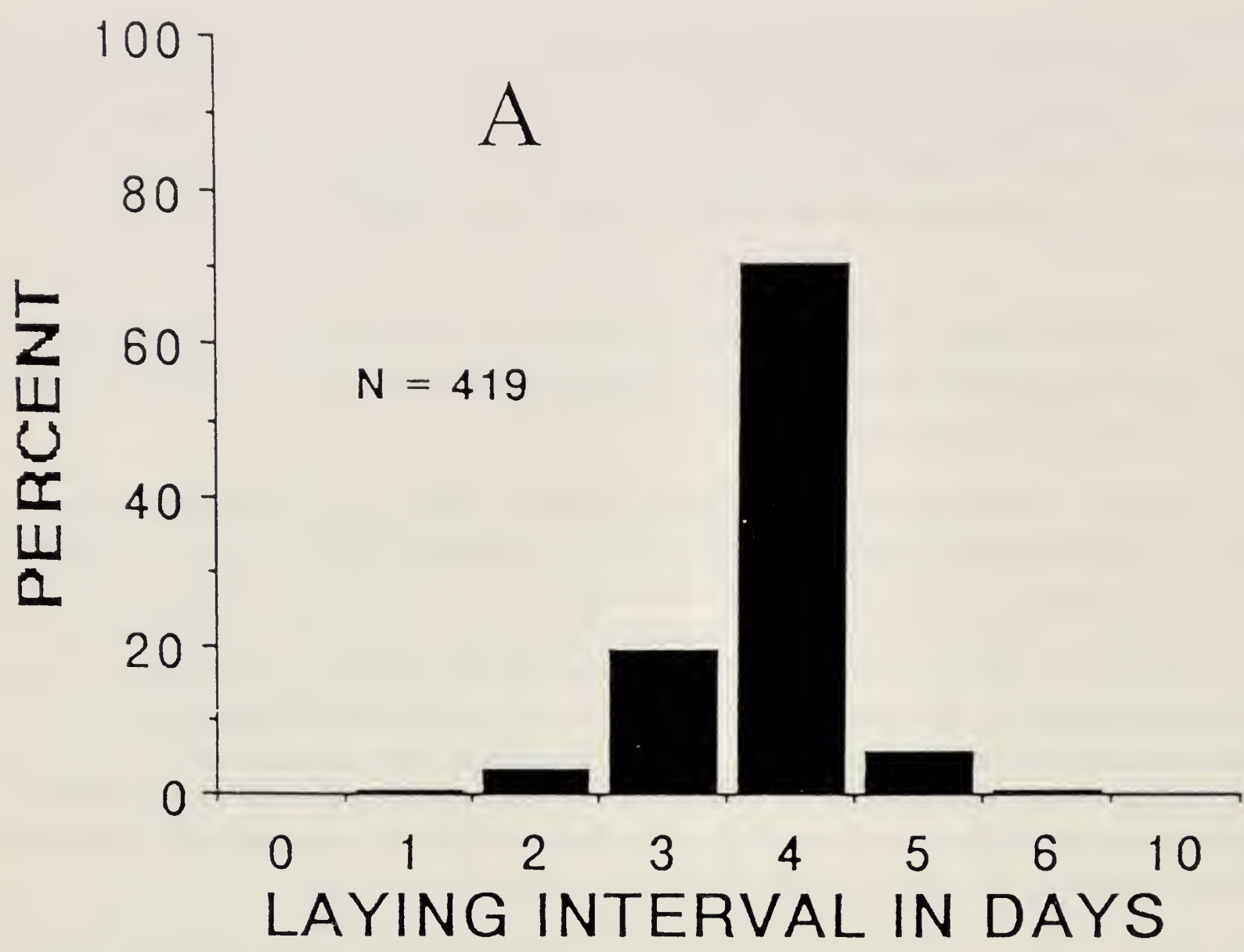


FIGURE 1 – The time in days that elapsed between the laying of the first and second eggs of Magellanic Penguins (A) and the hatching of these eggs (B).

13 day period averaged 5 (SE = 0.4, n = 20) in 1986, 8 (SE = 0.3, n = 15) and in 1985, 6 (SE = 0.3, n = 29). The frequency of nest reliefs was similar in 1985 and 1986 and in 1985 and 1987 (Mann Whitney U '85 to '86 P = 0.23, '85 to '87 P = 0.3) but exchanges were significantly longer in 1987 than in 1986 (U = 27, P = 0.001). Hatching asynchrony was similar in 1987 and 1986 and in 1986 and 1985 (P = 0.27, P = 0.18 respectively) but was significantly shorter in 1987 compared to 1985 (U = 436, P = 0.003).

TABLE 1 – Mean time (days) between feeds for Magellanic Penguin chicks over half-month periods during three breeding seasons at Punta Tombo, Argentina. Standard deviation is given in parentheses. N is the total number of intervals between feeds for each half-month period that was used in the calculation.

Date	1985-1986		1986-1987		1987-1988	
	X	N	X	N	X	N
Dec 1-15	1.5 (0.7)	161	1.4 (0.6)	146	1.9 (1.0)	80
Dec 16-31	2.0 (1.1)	118	2.3 (1.2)	89	2.2 (1.2)	172
Jan 1-15	2.3 (1.2)	103	2.6 (2.0)	81	2.4 (1.7)	148
Jan 16-31	2.2 (1.4)	126	2.2 (1.9)	106	2.1 (1.1)	163
Feb 1-15	2.3 (1.20)	59	2.4 (1.3)	68	2.0 (1.2)	120

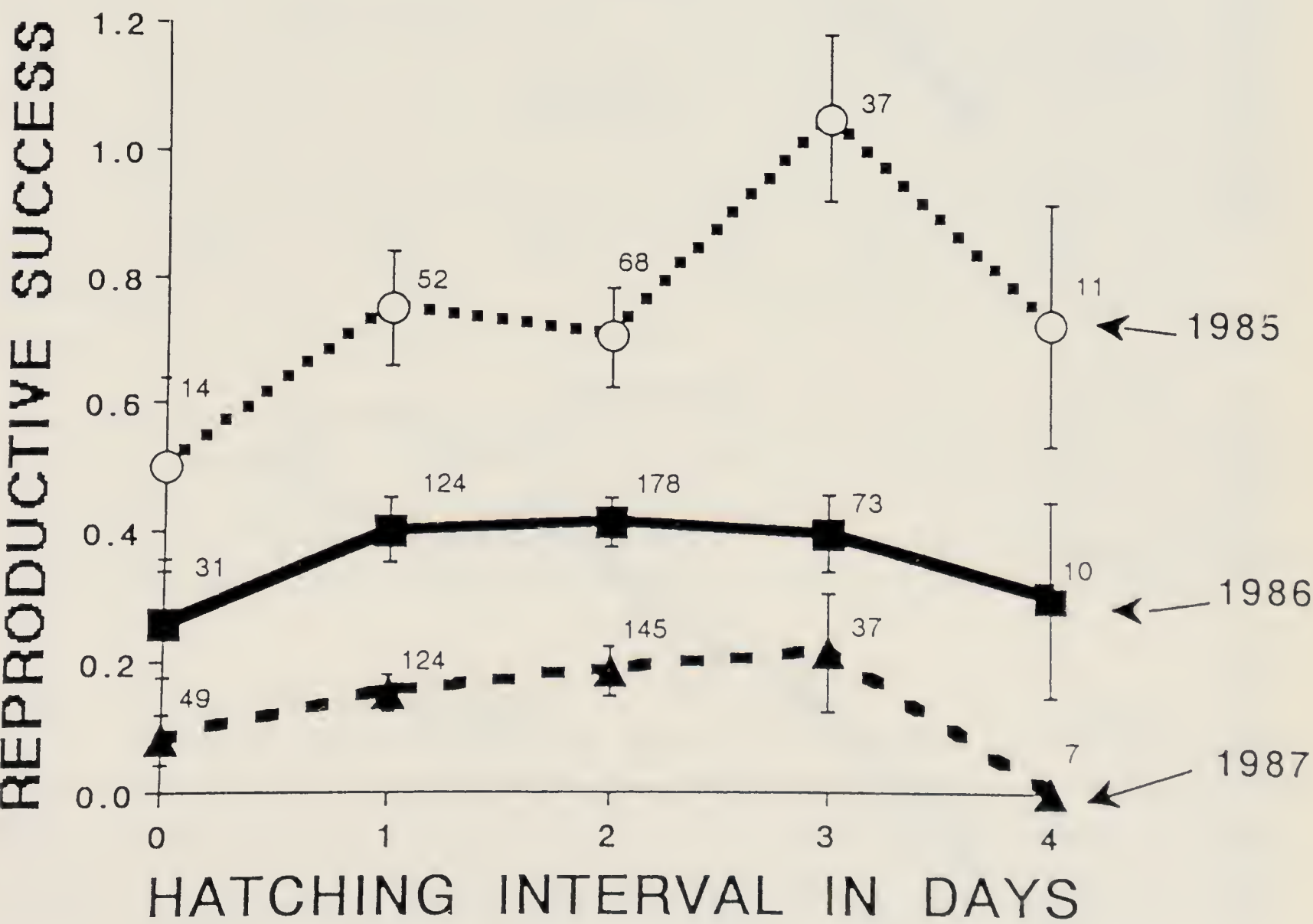


FIGURE 2 – Reproductive success of Magellanic Penguin nests in 1985, 1986 and 1987 with a hatching interval between the first and second egg of 0 to 4 days.

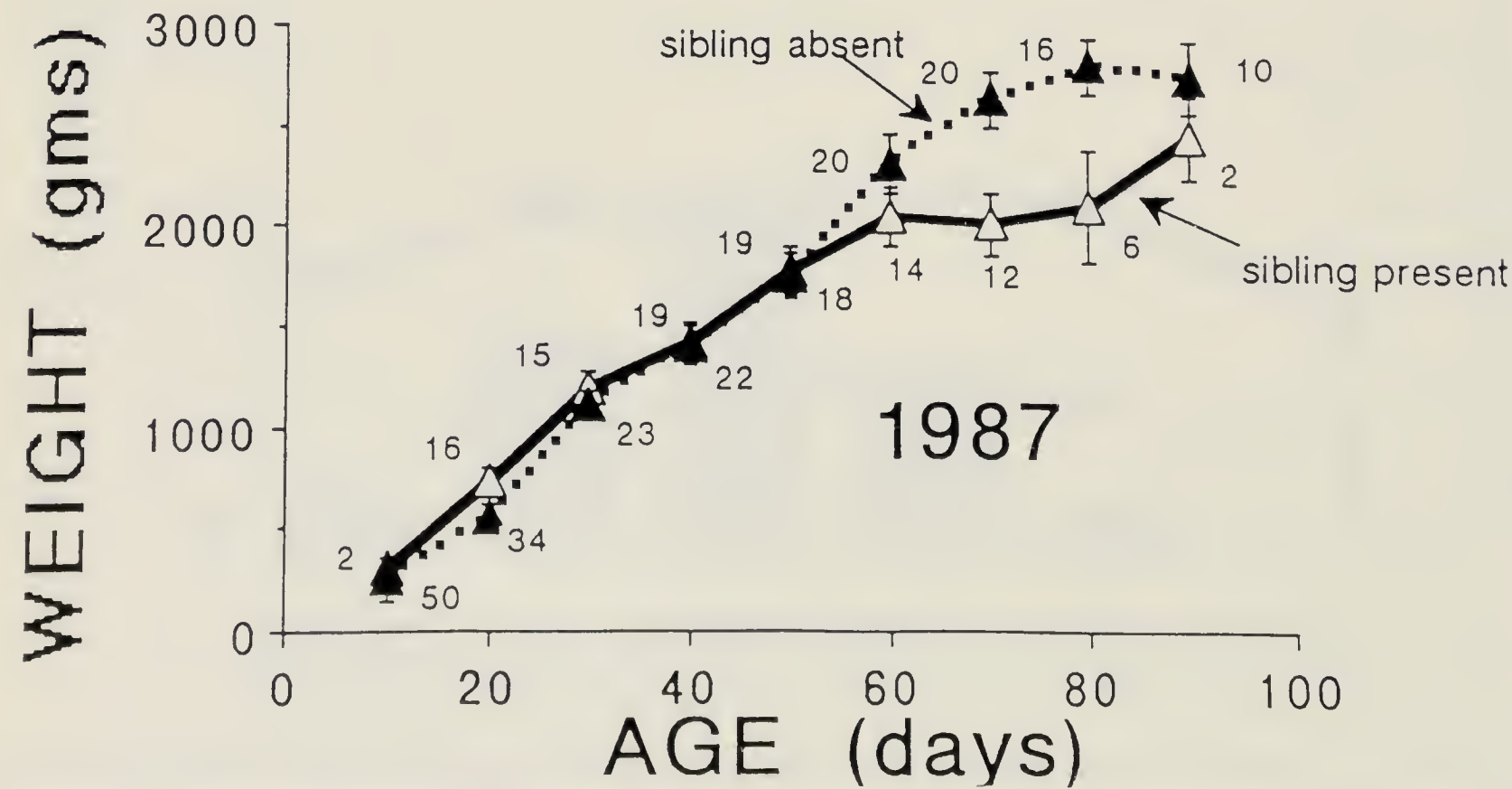
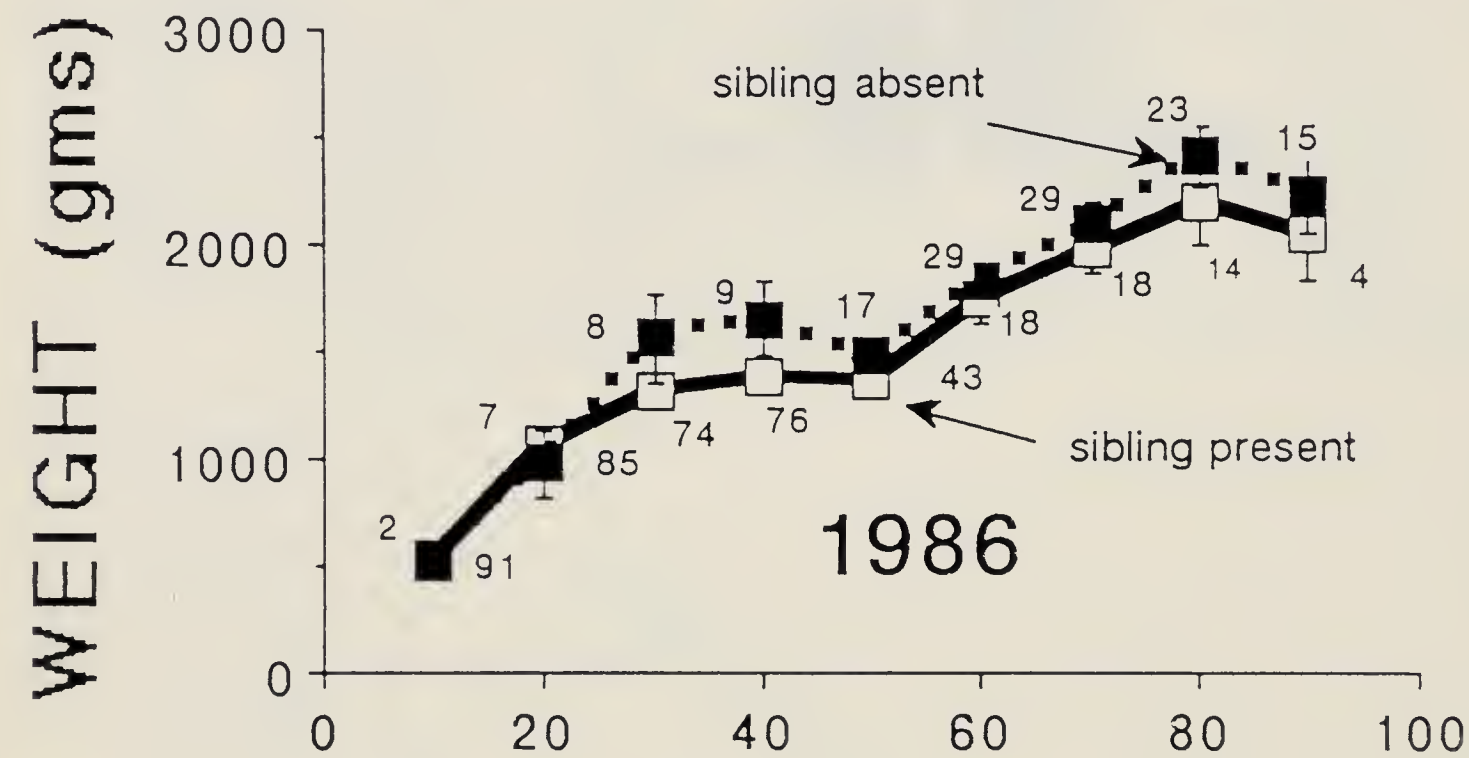
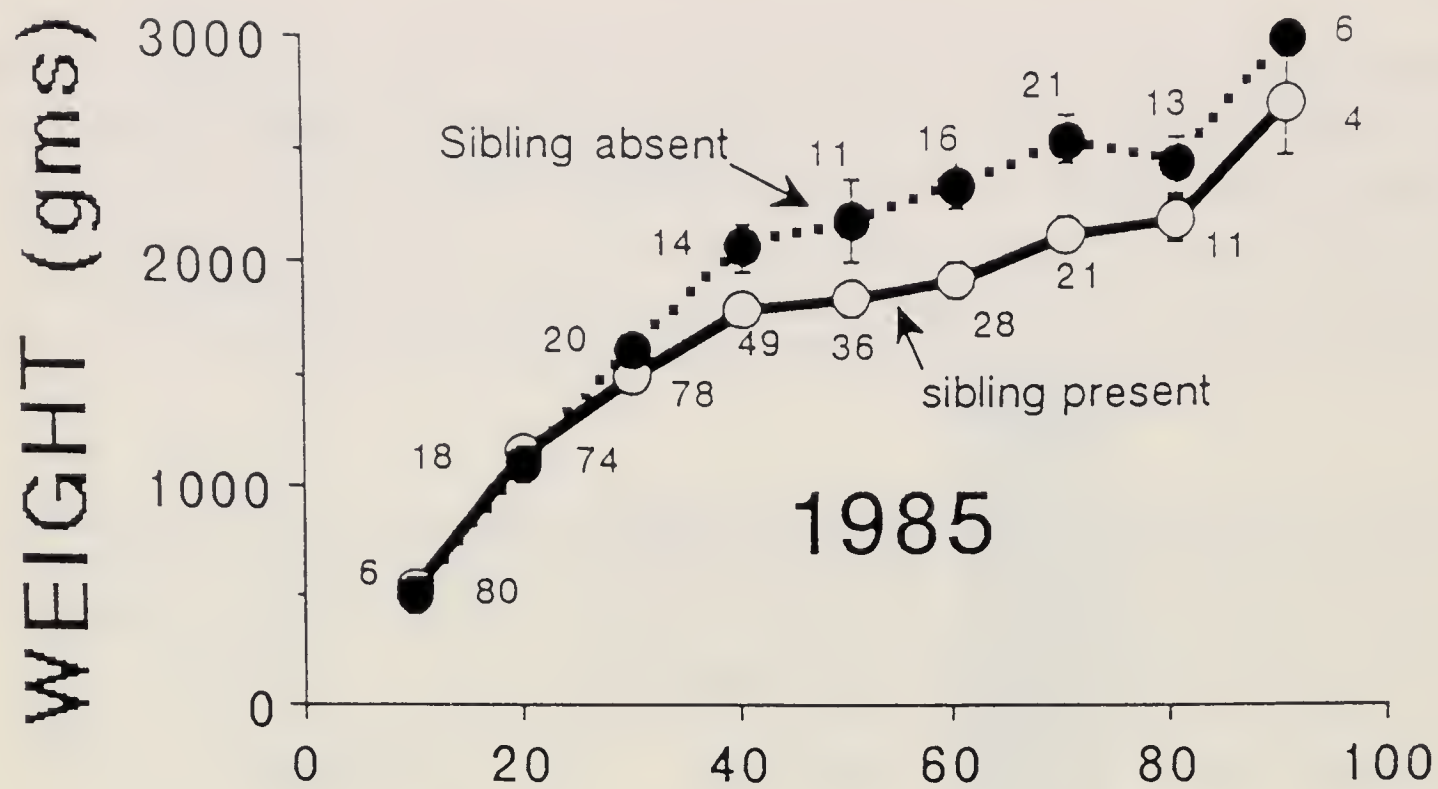


FIGURE 3 – Weight increase of nests with lone chicks (sibling absent) and nests with two siblings in 1985, 1986 and 1987. The age of all chicks were known within one day. Sample sizes are shown in small numbers next to each point and the standard error is plotted.

As the chicks age, adult foraging trips lengthened. In 1986 foraging trips, calculated as the time between feeds, for 23 to 30 November averaged 1 to 2 days ($x = 1.2$ days, $SD = 0.8$, $n = 83$). Foraging trips were variable among years suggesting food availability fluctuates (Table 1).

Reproductive success

Variability in reproductive success due to differences in asynchrony is small compared to yearly differences in success due to changes in food distribution and/or abundance (see Boersma et al. 1990). Pairs that hatch their chicks synchronously, on the same day, or most asynchronously, 4 days apart, had lower reproductive success in all years than pairs with hatching intervals of 1, 2, or 3 days (Figure 2). In 1985, the year with the highest overall reproductive success, survival was slightly higher for chicks that hatched 3 days apart than for those that hatched one or two days apart. In 1986 and 1987, there was no difference in reproductive success of nests that hatched eggs 1 to 3 days apart (Figure 2). In all three years, a few nests, those with hatching asynchrony of one, two or three days, fledged two chicks. Chicks that hatched two days apart lived longer than chicks that hatched at other intervals.

Growth of the siblings

For chicks between the age of 0 to 30 days, the period when one adult is normally present in the nest, the difference in the amount of food fed each sibling was not explained by hatching asynchrony or by size asymmetry. I examined this relationship by comparing hatching asynchrony and size asymmetry to the ratio of the weight of the first chick to that of the second before and after a feed. Analysis of variance showed that no significant part of the variance was explained by hatching asynchrony ($P = 0.62$) but that size asymmetry was significantly related ($F = 8.45$, $n = 148$, $P = 0.004$). Size asymmetry for chicks under 30 days old, however, explained only about 5% of the variability ($R^2 = 0.054$). Likewise, when chicks were 31 days or older, hatching asynchrony did not explain the variation in feed size between siblings. Again, size asymmetry was significantly related to how much weight first and second chicks gained after a feed ($F = 9.26$, $n = 113$, $P = 0.003$). Nonetheless, size asymmetry explained only 8% of the variation ($R^2 = 0.076$).

The growth of lone chicks was greater than that of chicks with siblings (Figure 3). However, the effect of a sibling on growth usually did not become apparent until 30 - 50 days after hatching. Differences between weight gains of single chicks and chicks in nests with siblings were most divergent late in the chick stage, when food demands of the young were highest (Figure 3). In all years, the cause of death for most chicks was starvation.

Sibling weight reversals

If greater mobility confers a competitive advantage, reversals in size hierarchy should be more common when second chicks are younger, less mobile, and presumably less able to compete. A reversal was scored when the size hierarchy between the chicks changed. If a second chick weighed more than the first on the day it hatched this was counted as a reversal. Subsequent reversals were scored each time the weight hierarchy changed. The number of size hierarchy reversals between first and second chicks was never more than 15% in any of the years.

In 1985, when food was most abundant, there were more reversals than in other years. The size hierarchy changed in 13% ($n = 779$) of nest checks of chicks under 30 days of age and 15% of the nest checks ($n = 1075$) of chicks more than 30 days of age. In 1986, 13% ($n = 2208$) of nest checks of chicks under 30 days of age and 8% of the checks of chicks more than 30 days old revealed a size reversal ($n = 1211$). In 1987, for chicks under 30 days of age, in 10% ($n = 1154$) of the nest checks the size hierarchy changed; in only 7% of the nest checks ($n = 467$) where chicks were more than 30 days of age was there a reversal. The evidence shows that chicks are unlikely to reverse their size relationships. When they do reverse, reversals are more common for chicks under 30 days of age, a time when they should be less able to compete with each other than when they are older.

In the study area checked daily, I examined the feeding pattern at the time of the reversal. Of 64 reversals, 52% occurred when the first chick was not fed until after the second one was born. First chicks that were not fed depleted yolk reserves, lost weight, and were smaller than the second chick by the time the second chick hatched. Another 48% of the reversals occurred when one of the chicks received most or all of a feed. Interestingly, this occurred several times after the first chick was not home, suggesting competition was unimportant in the reversal. On occasion ($n = 2$), reversals in weight occurred when the two chicks received similar amounts of food because the smaller chick lost weight more slowly than the larger first chick.

Parental feeding and sibling competition

When chicks are small they have little muscle control, are helpless, and seek out dark places, normally under the adult where they are brooded. They can lift their heads but can do little else. Adults regurgitate to the chick and chicks have little ability to out-position each other or thwart an adult's decision to give food to whichever chick it chooses. Thus, while a chick is young the adult has absolute control over the apportioning of food. As the chick grows, its mobility increases and its ability both to thwart adults and to compete should increase.

When the chicks are young and immobile, the adult hunches over the chicks to feed them. When the chicks are mobile, the adult no longer feeds in this position but, instead, prevents them from gaining direct access to the bill by holding the chicks back with its flippers. Chicks try to get to the front of the adult but the adult prevents this by turning. The adult regurgitates to one side and then to the other (i.e. alternating from left to right). Chicks must stretch their bodies and necks over the adult's flippers and put their bills into the adult's to be fed. Often the chicks stand on tiptoe and push against the adult to get as close to the bill as possible. Often when there is only one chick, the chick begs on one side of the adult and then runs to the other side when the adult bends to regurgitate to that side.

When only one chick was present, the adult normally continued to regurgitate on alternate sides but was more apt to feed the chick on only one side or with the chick in front. In 5 feeding bouts where only one chick was present, the adult fed to the front or to only one side for 74% of the feeds ($n = 38$ feeds). In the other 26% of the feeds, the chicks switched sides. During 22 bouts where two chicks were present, the adult fed to both sides. Only once in 262 feeds did an adult feed to the front when two chicks were present.

Adults fed significantly more often to the side of the larger chick ($\chi^2 = 12.87$, $P < 0.001$, $n = 6$ feeding bouts). When the chicks were of equal size the adult fed the chicks more equally ($\chi^2 = 3.57$, $P > 0.05$, $n = 3$ feeding bouts).

In 6 of the 22 two chick feeding bouts, chicks switched sides 4 or more times. In one feeding bout, the smaller chick got only 1 of the first 7 feeds but got all of the last 4 feeds when the larger chick quit begging. In another feeding bout the larger chick got all of the first 5 feeds but the smaller chick got the last 7 feeds after the larger chick became satiated.

The adult appeared to be exercising a preference for the larger chick in the majority of feeding bouts because when it bent its head to regurgitate to the side the small chick was on, the adult was less likely to regurgitate than when it bent its head to the side where the larger chick was. Chicks likewise seemed to exercise some control when they were 70 or more days of age, either because they broke up feeds or got their beaks into the adults' throat when the other chick was feeding. In one feeding bout the smallest chick consistently went under the adult's neck when it tried to regurgitate to the larger chick and was successful at breaking up several of the feeds. Nevertheless, the larger chick got longer feeds and seemed to get more food at each feed than the smaller chick. In one bout, a small chick jumped under the adult's bill, climbed to the other side and successfully broke up several feeds. However, the adult still fed the larger chick more than the smaller one. In sum, chicks seemed unable to control which the adult fed.

When chicks switched to different sides of the adult throughout the feeding bout, the feeds to both chicks were not different ($\chi^2 = 2.05$, $P > 0.05$, $n = 4$ feeding bouts). Adults appeared to be able to keep chicks behind their flippers so that the largest chick was fed first and fed until it was less insistent. Chicks never pecked or threatened each other during feeding bouts.

Occasionally an adult appeared to feed a chick that was not its own. Such stealing of food was uncommon but happened when chicks were large and mobile, about one month before fledging.

In one case, an adult returned to feed a chick that had just been fed by its mate. The chick peeped for food very slowly and quietly but it was fed immediately. When the chick quit begging the adult walked around the nest and was greeted by a chick that ran out of a burrow and began begging rapidly and loudly. The adult attempted to bill duel with the chick (bill knocking), slapped it forcefully with its flipper and then fed it once. The chick continued to beg as the adult moved toward its burrow. After another flipper slap, the chick was fed a second time after which the adult returned to its own chick, which still did not beg for any more food. Such stealing of food is probably rather insignificant to the adult's fitness since adults rarely feed chicks other than their own. Perhaps this most frequently occurs when the adult's own young are absent or dead.

Normally, intruding chicks stand with the adult's chicks, make all the begging head wobbles and other movements but are silent. On occasion, perhaps less than 10% of the time, an intruder received some food. Most often these chicks were larger than the adult's chicks. If a strange chick peeped, the adults generally stopped feeding,

pecked the chick and drove it away. These chicks almost never got more than one partial bill full, suggesting adults rarely lose control. When chicks were large and switching sides the adult was more likely to drop food which was not eaten by the chicks. Competition among the siblings as they switched sides increased food loss and appeared to reduce the efficiency of food transfer.

There was one case where the identity of both parents was known at the feeds and where a reversal in size occurred. In this instance, the male fed the largest chick first (#1). At the next feed where a reversal occurred, the female fed the smaller second chick (#2) more. Even though the #2 chick now weighed more than the #1 chick, when the male returned it fed most of its food to this now smaller #1 chick, causing another reversal. The female returned for the next two feeding bouts and fed the smaller #2 chick more. At the next feed the male who had previously been feeding the #1 chick more fed the #2 chick more. This suggests that individual parents may have different preferences for which chicks they feed and that this behavior can cause size reversals. It also suggests that adults, and not chick size, control which gets fed.

DISCUSSION

The adults' incubating behavior reduces the effects of laying asynchrony. Adult feeding behavior reduces size asymmetry caused by hatching asynchrony and divides the food between the first and second chicks equitably when food is available and inequitably when food is scarce. Even with these behaviors, the size hierarchies remain and are generally stable throughout the hatchling period. This suggests that chicks have little ability to alter the effect of their hatching position through competition.

Food appears to be a limited resource since there is a difference in the average growth of lone chicks versus chicks with siblings (Figure 3). However, evidence suggests that competition is of little importance in determining the outcome of which chick survives. Adults prefer to feed the larger chick. Chicks were not able to change this adult preference to feed the larger chick. Even very large intruder chicks from other nests were unable to control which the adult fed. There is no evidence that chicks intimidate each other. These facts suggest that adult feeding preferences are more important than sibling competition in determining what chick survives.

Reversals in size hierarchies occurred predominantly when the first chick was not fed until after the second chick hatched. Hatching order and being fed first were important variables in determining whether the first or the second chick was in the most favorable position for survival. Mechanisms that tend to favor the survival of the first chick over the second include hatching asynchrony and size asymmetry. Hatching asynchrony appears to be related to the interval between nest reliefs to increase the probability that both chicks will be fed before they lose much of their yolk reserves. The two-day hatching interval, more than all other intervals, increased the first and second chick's lifespan (Boersma, unpub. data).

Hierarchies may be important in helping adults apportion food most efficiently because they can favor one chick over the other. For Magellanic Penguins, synchrony and maximum asynchrony resulted in lower reproductive success, suggesting that either extreme reduced adult fitness. What are the costs of asynchrony?

Hahn (1981) proposed that synchrony would increase the intensity of sibling competition. Theoretically, synchrony should promote fighting because competitors are more evenly matched (Maynard Smith & Parker 1976). In Magellanic Penguins, and perhaps in most other species, increased asynchrony rather than synchrony should increase competition among offspring and interfere with the adult's ability to distribute food efficiently. Competition and interference by nestlings, through jostling and breaking up feeds, should increase food demands since energy must be used to out-position or fight with a sibling. When Magellanic Penguin chicks are larger, the adults are more likely to drop food and feed young that are not their own. When food is limited, such sibling competition should not be in the parents' best interest since energy is wasted and the cost of rearing the chicks increased.

Studies on other birds have shown that increased synchrony, by artificially creating more synchronous hatching, increased reproductive success (Bryant & Tatner 1990). Werschkul (1979) found in experimental broods of herons that even-aged broods grew as fast as older chicks from asynchronous broods and attributes the success of more even-aged broods to the adults' ability to distribute food more equally among the nestlings. He concluded that in asynchronous broods, parents were unable to distribute food equally because older and larger siblings hoarded the food by consuming more than was necessary for growth. Interestingly, most studies have failed to find that asynchronous hatching increases reproductive success and many studies have found synchrony enhances success (see Amundsen & Stokland 1988). This may be because, through sibling competition, food is distributed more equitably.

Adults should apportion the food to the healthiest and largest chick first and then to the second chick. This is apparently what Magellanic Penguins are doing since, in years of poor food (1987), second chicks died earlier than in other years. The rise in second chick death between the age of 50 and 70 days (when food demands of the first are higher than when it was younger) also suggests that adults feed first chicks first and second chicks get what is left over (Boersma, unpub. data). Thus, adults appeared to give "excess" food to the second chick. When food is limited, it would be in both the adults' and the largest chick's interest to feed the smaller chick only after the needs of the largest are met.

Herbert & Barclay (1986) found that first gull chicks were fed before later hatchlings and suggested that in the absence of a feeding hierarchy, parents cannot control which chick receives food. They suggested that parents may control feeds because older and larger chicks could follow parents more closely than younger and smaller chicks.

In Magellanic Penguins and the other Jackass Penguins, chicks compete to be on the side where the adult disgorges food. Chicks of several bird species compete for the preferred feeding position (Ryden & Bengtsson 1980, Greig-Smith 1985). When Magellanic Penguin chicks are too similar or too different in size, adults lose control of who they feed. In sum, Magellanic Penguin parents, more than chicks, appear to control which gets fed and which survives. Asynchronous hatching, often the proposed mechanism of brood reduction, is strongly determined, for Magellanic Penguins, by nest relief and appears to function not as an important mechanism in brood reduction but as a mechanism to maximize the chance that both chicks will be fed soon after hatching.

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INFANTICIDE OR ADOPTION BY REPLACEMENT MALES: THE INFLUENCE OF FEMALE BEHAVIOUR

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ABSTRACT. Replacement males of some species adopt or are indifferent to the young sired by the previous male while in other species they commit infanticide. Patterns of adoption versus infanticide emerge when comparing different species, but little is known about the occurrence of variation in these traits within species. Tree Swallow *Tachycineta bicolor* males which replace a breeding resident during egg-laying or early incubation adopt the nestlings, but those that arrive in later incubation or when there are nestlings in the nest kill the nestlings that were sired by the previous male. Females are receptive and copulate with replacement males that arrive during laying or early incubation but are aggressive to those that arrive later. Frequent copulation and copulation after clutch completion with the replacement male may be tactics by which widowed females decrease the likelihood of infanticide and enhance the probability of paternal investment through increasing the confidence of paternity.

Keywords: Tree Swallow, *Tachycineta bicolor*, infanticide, adoption, prolonged copulation, certainty of paternity, confidence of paternity, sexual selection, parent-offspring.

INTRODUCTION

Infanticide, the killing of dependent, conspecific young, can be an adaptive behaviour, moulded by natural selection, in which some advantage is gained by the infanticidal individual (Hrdy 1979). Sexually selected infanticide, where offspring of another individual are killed in order to gain a breeding opportunity, appears to be more common in birds than previously realized (Robertson & Stutchbury 1988). A frequent pattern of sexually selected infanticide involves a floater male which evicts or replaces a resident, kills the infants that were sired by the previous male, and then mates with the widowed or a new female (Hrdy 1979, Crook & Shields 1985, Freed 1986, Møller 1988a, Robertson & Stutchbury 1988). In a review of conditions which select for infanticide versus adoption, Rohwer (1986) predicts infanticide by replacement males is more likely to occur in species which maintain the pair bond and reneest following nest failure, while adoption is predicted in species which maintain the pair bond and have a second brood following successful nesting, but which disperse following failure. Further analyses of existing studies by Meek & Robertson (in prep.), however, indicate that full adoption is very uncommon in birds.

Infanticide by male birds poses a conflict of interests between the sexes. The infanticidal male benefits by the breeding opportunity created, but the female must pay the cost of time and energy required for reneesting. Natural selection should favour counter-tactics by females which function to prevent infanticide by males (Andelman 1987, Freed 1987, Møller 1988a). One such counter-tactic may be for females to increase the male's confidence of paternity (perceived paternity) in cases where his genetic paternity is low or even zero. From the female's perspective, engaging in frequent copulations and copulating throughout egg-laying when one or a few copulations would suffice to fertilize all the eggs, or even copulating after egg-laying, may influence the

replacement male's confidence of paternity and hence his decision of whether to adopt or kill the nestlings.

Sexually selected infanticide, in which the selective advantage is accrued through gaining a breeding opportunity (e.g. mate or nest site) is most likely to evolve in species which face limited opportunities for breeding (Robertson & Stutchbury 1988). Limited availability of nest sites, or other resources that are required for breeding, results in a floater population in which individuals compete for a chance to breed. Residents which are killed by predators or evicted are quickly replaced. Selection then favours behaviour by the replacement which increases the likelihood that the new-found breeding opportunity will result in successful reproduction. In a short-lived, single brooded species which does not disperse after nest failure, selection will likely favour infanticide (Rohwer 1986), since there is a large disadvantage to delaying breeding (Studd & Robertson 1985).

Tree Swallows *Tachycineta bicolor* are secondary cavity nesters which face intense competition for limited nest sites, typically old woodpecker holes, but they breed readily in nest boxes. They have large floater populations of both females (Stutchbury & Robertson 1985) and males. Experimental studies have established that replacement male Tree Swallows which arrive when there are young nestlings or advanced incubating eggs in the nest kill the nestlings and mate with the widow or a new female (Robertson & Stutchbury 1988, Robertson 1990).

My objectives in this study were first to further examine the effect of nest stage on the male's decision of whether to adopt or kill the eggs or nestlings, and second to explore the possibility that female behaviour, especially prolonged copulation, might function as a tactic to avoid infanticide by replacement males.

METHODS

These studies were done in grids of nest boxes in open fields and over water at the Queen's University Biological Station in southern Ontario, Canada, from 1985 through 1990. Each year, females and most males were captured and uniquely marked with acrylic paint.

Naturally occurring replacements, where a vacancy arises due to predation or death from other causes or where a resident is evicted by another male, are quite rare. To create situations where replacements would occur and infanticide might be expected, resident males were permanently removed from certain experimental nests. Removals were done during the egg-laying, incubation and nestling stages so the behaviour of the female and of replacement males arriving at different stages of the nesting cycle could be examined. Experimental and control nests were watched to determine copulation frequencies and feeding rates.

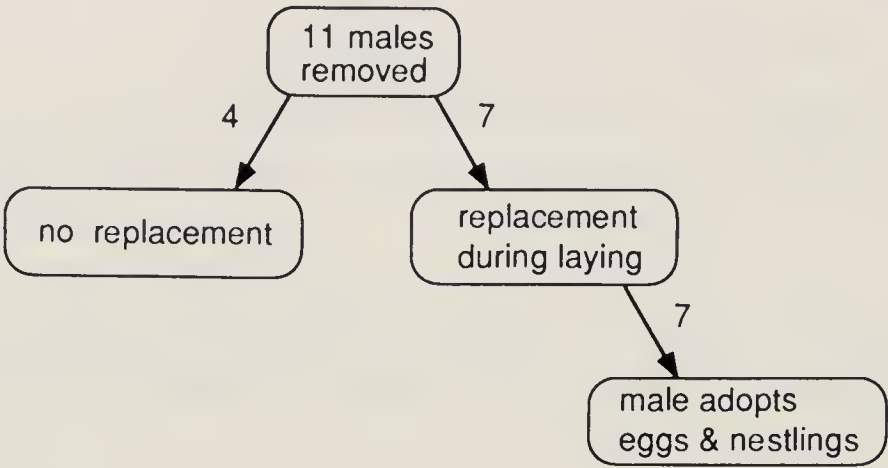
RESULTS

Adoption or infanticide by replacement males

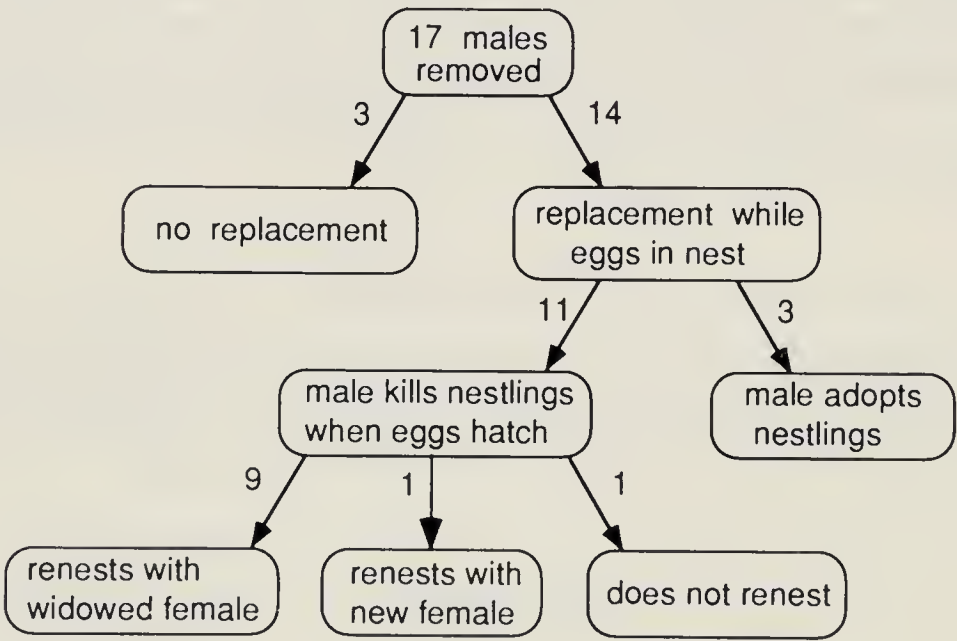
EGGLAYING. Replacement males arriving during the egg-laying period adopt. Seven replacements occurred following removal of males from 11 nests during egg-laying. Six

of the seven had some possibility of partial genetic paternity of the brood since they arrived prior to the last egg being laid. All seven males adopted the brood (Figure 1a).

(a) Egg-laying



(b) Incubation



(c) Nestling stage

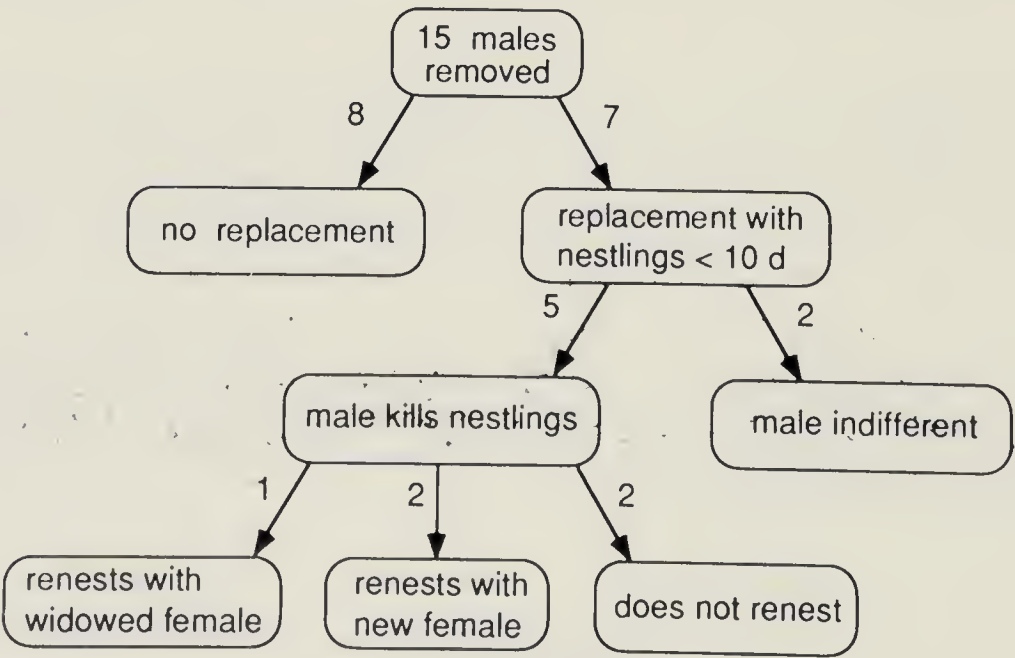


FIGURE 1 - Outcome of male removal experiments with replacements arriving during (a) egg-laying, (b) incubation, and (c) the nestling stage.

INCUBATION. Replacements during incubation usually adopt if they arrive early, but commit infanticide if they arrive late in incubation. Males were removed from 17 nests during incubation and 14 replacements occurred. Replacements frequently enter the nest cavity so must be aware of the nest contents at the time of their arrival. All 14 defended the nest while incubation continued. None disrupted the nest or eggs. Three of these 14 replacement males, all of which arrived on day two of incubation, adopted the nestlings when they hatched. However, 11 of the replacements, eight of which arrived on day 5 or later in incubation, killed the nestlings soon after the eggs hatched. Ten of these 11 infanticidal males subsequently renested (Figure 1b).

NESTLINGS. Replacements arriving when there are young nestlings usually commit infanticide. Resident males were removed from a total of 15 nests which contained nestlings 1-2 days old. In seven cases a replacement arrived, in all cases nestlings were less than 10 days old. Five of these males killed the nestlings by pecking them, or by removing live nestlings and dropping them outside the nest box. The other two replacement males were considered indifferent in that they neither harmed nor helped feed the nestlings. Three of the five infanticidal males renested, two with new females and one with the widowed female (Figure 1c).

These results indicate that the timing of the replacement male's arrival is important in determining whether he adopts or kills the brood. Males which arrived before the clutch was complete, such that they had a reasonable possibility of fertilizing at least one egg, always adopted the nestlings. Males which arrived shortly after clutch completion, such that there should have been low (or zero) confidence of paternity, either adopted or killed the nestlings, depending upon when they arrived. Males which arrived well after clutch completion, or during the nestling period, so there was no opportunity to sire any of the young, usually killed the nestlings. Surprisingly, males which arrived after clutch completion did not disrupt the clutch, but rather waited until the end of the 14 day incubation period and then killed the nestlings soon after the eggs hatched.

Prolonged copulation and adoption as a possible counter-tactic

Females are often aggressive to the replacement male upon his arrival, and female aggression may have prevented infanticide by the two so-called "indifferent" replacements. In the absence of a resident male, the aggression of the female toward male "intruders" declines rapidly, and within an hour to a day or more of his arrival, the female is receptive and copulates with the replacement male. In nine of 14 cases where replacement males arrived during incubation, females were seen to be receptive and copulate with the replacement.

To determine whether copulation patterns of females with replacement males were different from those of control pairs, one grid of 18 boxes was watched regularly from mid-April to mid-May 1989 and copulations were recorded. Copulations occur most frequently on top of the nest box or at a nearby perch, with the male hovering just above the female while giving a characteristic chatter. The male intermittently alights on the female's raised wings as she assumes a crouched position, lifts her tail and cloacal contact is made. Each copulation bout involves from one to ten or more cloacal contacts with the male hovering briefly above the female between each one.

Copulation by mated pairs begins up to 19 days prior to laying of the first egg, with the frequency of copulation increasing to a broad peak during the week before

laying begins when pairs copulate on average about once every 2 hrs (Figure 2). Copulation frequency declines at the onset of laying, and no copulations were observed for the control, mated pairs after clutch completion.

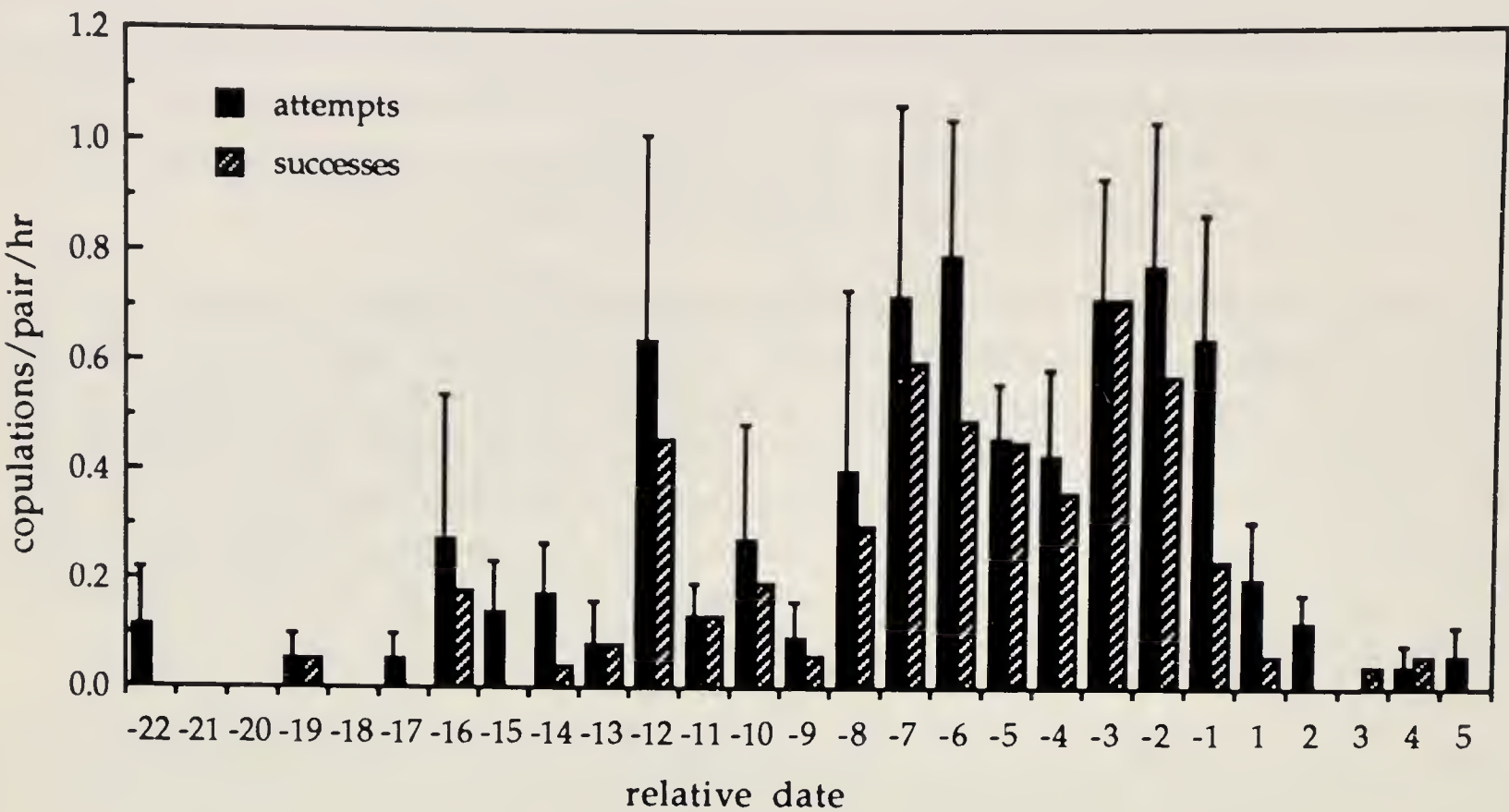


FIGURE 2 - Copulations per pair per hour for 18 pairs of Tree Swallows in Hughson's Grid watched regularly from mid-April to mid-May 1989. Relative date is in relation to clutch initiation where first egg is laid on day 1.

Throughout the period copulations occur, the number of cloacal contacts per copulation bout averages about four, with a trend toward an increase as egg laying approaches (Figure 3). The number of cloacal contacts might serve as an indicator of either female receptiveness and/or male persistence.

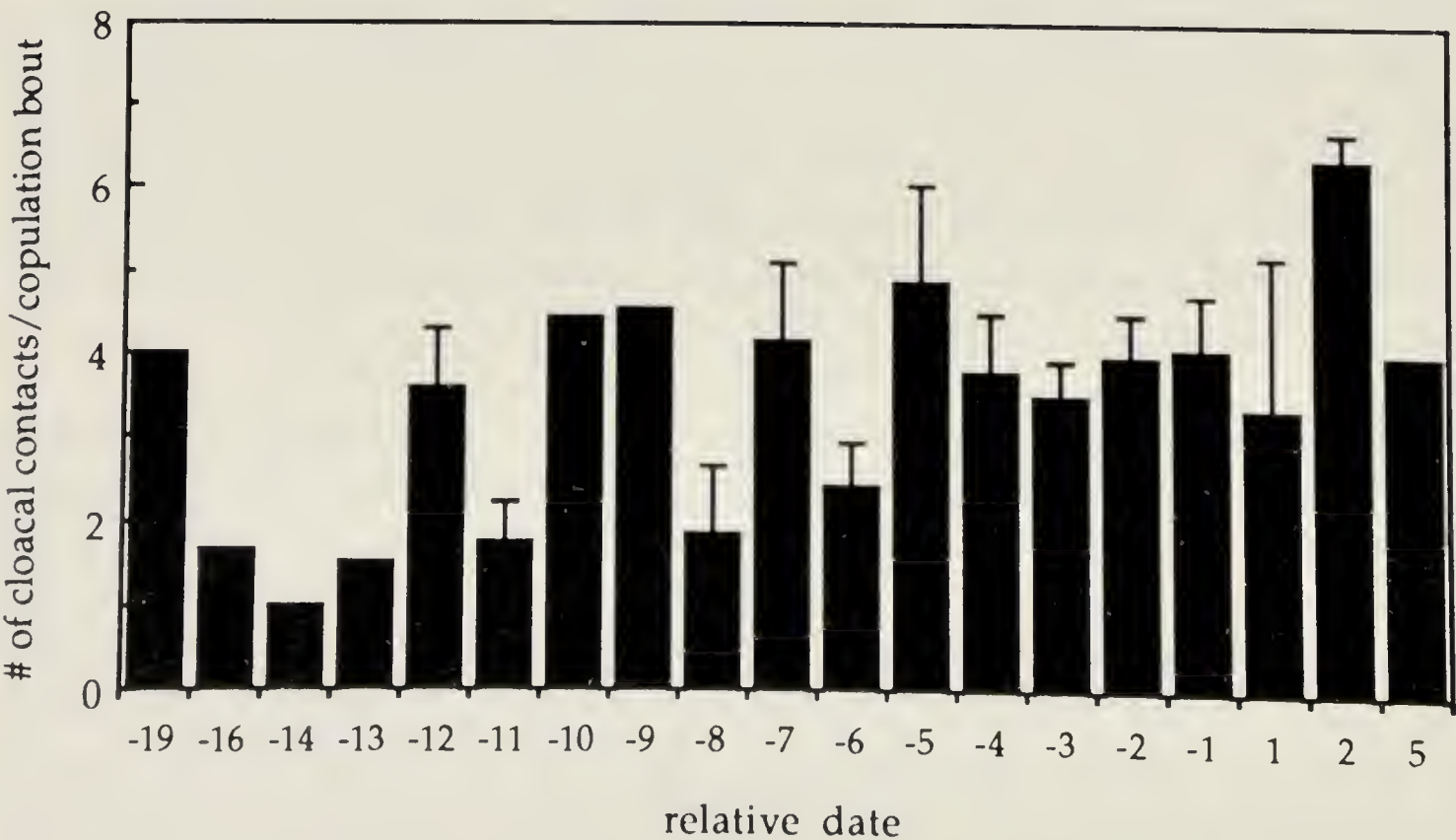


FIGURE 3 - Number of cloacal contacts per copulation bout in relation to first egg date (day 1).

The nine cases in which replacement males copulated with the resident female during incubation were unique to replacement pairs. Control pairs did not copulate after clutch completion. The copulations with replacements, which occurred as late as the day before hatch, were otherwise normal in that they averaged approximately six cloacal contacts per copulation. Obviously the incubation stage females were receptive to the replacement males even though they laid no additional eggs and continued to incubate the eggs which had been fertilized by the previous male. Although there were no apparent differences in the copulation behaviour of incubating females compared with females in their fertile period, the facts that the females were incubating when the replacement male arrived, and that the male inspected the nest, should be useful cues to the replacement male to allow him to avoid adopting unrelated young.

In cases where the replacement male arrived during egg laying, copulation may have resulted in fertilization of some of the clutch, so in fact the replacement male may have had some share in the paternity of the brood. To test whether the males which replaced during egg laying and adopted the brood were fully adoptive or whether they adjusted their paternal care in relation to their certainty of paternity, feeding rates of six pairs where the replacement male arrived after laying of the second egg and before completion of the clutch were examined and compared with those rates of control pairs with the same brood size and hatch dates.

The mean daily proportion of all feeding trips made by the male, for experimental pairs with replacement males, and for matched control pairs shows that in no case was there a difference in the extent of care by the adopting replacement, compared with the control male (Table 1). These results indicate that adoption, where it occurs, is complete. Since these replacement males could have fertilized at most three of the six eggs in a clutch, these data indicate that Tree Swallows do not adjust their paternal care in relation to their certainty of paternity.

TABLE 1 - Mean daily proportion of all feeding trips made by the male.

Pairs' identity (Control-Replacement)	Proportion of trips by male	
	Control	Replacement
HUA3-CS5	0.30	0.43
CS11-RO2	0.55	0.31
SC1-CS7	0.52	0.50
HUC7-HUB6	0.62	0.49
NSU4-NSV3	0.59	0.55
NSB2-MST3	0.64	0.58
MEAN	0.54	0.48

DISCUSSION

Are female Tree Swallows which copulate with replacement males during egg laying and throughout incubation involved in tactical deception which results in the male having an unrealistically high confidence of paternity? Replacement males which are not infanticidal, and which adopt the brood, appear to provide as much parental care

as control males with full genetic paternity. Therefore, if by copulating with a replacement male a female is able to provide even a small possibility of paternity and/or an increased confidence of paternity, it may be sufficient to both prevent infanticide and secure full-scale paternal care of the entire brood through adoption. However, if prolonged copulation does function to confuse paternity and increase the chance a replacement male will adopt, it does so effectively only during early incubation. All cases of males arriving in late incubation led to infanticide.

Infanticide is clearly adaptive for males which replace a previous resident during the incubation or nestling stage. Floater males which do not breed have no reproductive output in the current year. In contrast, most replacing males which are infanticidal do obtain a breeding opportunity. Of 18 replacement males which killed nestlings, 14 renested and 11 of them fledged at least one young that year.

Infanticide by replacement males also occurs naturally in these populations. During this study, there were four cases, out of approximately 100 nesting attempts monitored, where resident males disappeared. In most cases, replacement likely occurred after the resident male was preyed on. A Sharp-shinned Hawk *Accipiter striatus* was frequently seen in the area and has been observed pursuing Tree Swallows. Although replacement by eviction is probably not common, it may occur occasionally. In all cases, the replacement males which arrived during incubation killed the nestlings on the day that they hatched. Clearly, infanticide as a means of gaining a breeding opportunity is an evolved component of the male Tree Swallow's reproductive strategy.

Adoption is adaptive for the replacement male only if he arrives during egg-laying so there is some possibility of fertilizing at least one egg. Males which arrived after clutch completion but yet adopted the brood were apparently behaving in a maladaptive manner since they did not fledge any of their own offspring in the current year. Interestingly, even early arriving adopting males, which at best shared a relatively small portion of the paternity of the brood, contributed as much parental care in feeding nestlings as control males. Brown (1983) also found that male Purple Martins *Progne subis* which replaced during or after egg-laying and probably had little or no share in the paternity of the brood aided in rearing young that were not their own. In contrast, Møller (1988b) has shown that male Barn Swallows *Hirundo rustica* appear to adjust the extent of their care to their certainty of paternity. The fact that Tree Swallows do not similarly adjust paternal care suggests that males may have been given an unrealistically high confidence of paternity by the female's prolonged copulation behaviour and this resulted in their adopting the brood. Gjershaug et al. (1989) argue that widowed Pied Flycatchers *Ficedula hypoleuca* copulate even though they have a full clutch or brood as a means of obtaining male parental care. I suggest that the prevention of infanticide may have an even more important influence on the evolution of prolonged copulation behaviour by widowed females.

For females, it is always advantageous to have the replacement male adopt, especially where lone females are unable to rear a full brood without male help. If the replacement male adopts, it not only increases the female's chance of fledging her current brood, but also saves her the time and energy required for renesting were the male to kill the nestlings. The fact that females confronted with a replacement male become receptive and copulate at the same time they incubate, while control pairs do not copulate after clutch completion, suggests that the receptivity of the female may

be functioning to manipulate the male's behaviour. Copulation with replacement males is not necessarily just a part of pair formation, since pair formation in early spring occurs without copulation behaviour.

An alternative explanation for the occurrence of copulation with replacements after clutch completion is that the behaviour is driven by the males, not the females. Hormonally, a male which has just acquired a nest site and a mate would be at an early stage of his reproductive cycle and thus ready to copulate. If the female behaves inappropriately, she may risk eviction by the male. However, whether copulation is instigated by the male or the female, the female's receptiveness would be functioning to prevent disruption of her current breeding attempt.

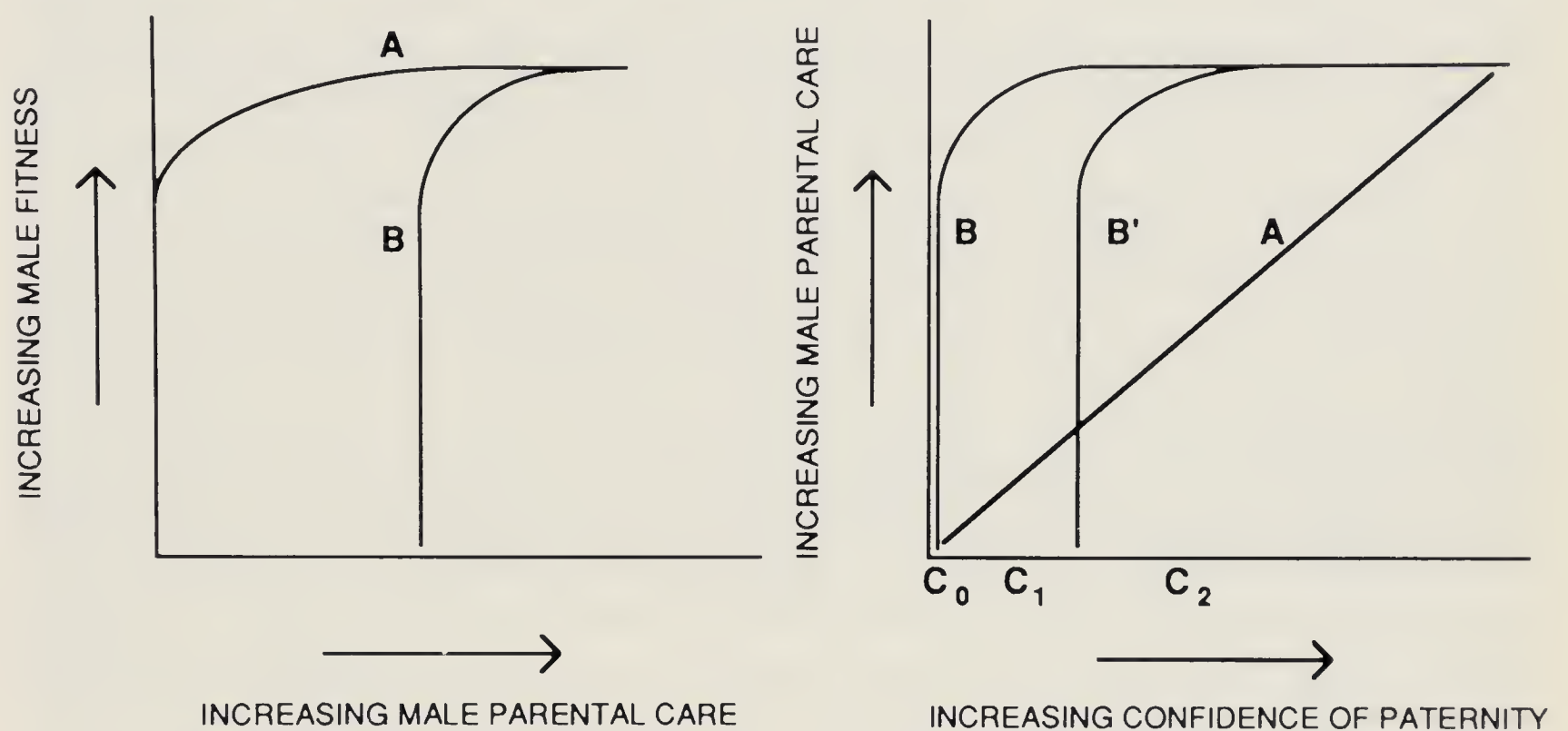


FIGURE 4 - a. Alternate extremes of the spectrum of the relationship between male fitness, measured by fledging success, and male parental care. In A, reduction of male care is not detrimental to nestling survival as may occur if the female or other individuals compensate. In B, reduction of male care has a strong negative effect on offspring survival.

- b. Predicted relationship between level of male parental care and confidence of paternity as determined by effect of male parental care on offspring survival (as above). When level of male care does not strongly affect offspring survival because a reduction of care is compensated by others, the male adjusts his level of care to his confidence of paternity (line A). If a reduction in male care is not compensated, the male provides full care regardless of his confidence of paternity, until some threshold of low confidence of paternity is reached, at which point he stops providing care. The level of the threshold (B versus B') may depend on the value to the male of other mating options. Prolonged copulation may increase the male's confidence of paternity, e.g., C_0 to C_1 , or C_1 to C_2 , and prevent him from reaching the threshold at which he would stop caring for the young (modified from Whittingham, Robertson & Dunn, in prep.).

Male Tree Swallows which replace during egg-laying and early incubation could avoid the apparent error of caring for unrelated nestlings if they destroyed any eggs in the nest at the time of their arrival. This would also save them the time of up to two weeks between arrival and hatch. Although Tree Swallows may have difficulty removing intact eggs, they can and do remove eggs that are only slightly broken, and females will build a new nest over a used nest containing eggs or dead nestlings. Therefore, it seems replacement males should be quite capable of disrupting a breeding attempt during the egg stage. Why replacing males do not destroy eggs already in the nest

at the time of their arrival is puzzling, but again it could relate to the sexual receptivity of the female and the male possibly being deceived as to the paternity of the brood. Interestingly, replacement male Barn Swallows which arrived during incubation also waited until the young hatched before killing them (Crook & Shields 1985).

Although prolonged copulation may give a male an inflated confidence of paternity and induce him to provide full care to unrelated young, it may be that the best option for a male with even a small probability of paternity is to provide the full normal complement of about 50% of the feeding visits to the entire brood. A graphical model to illustrate this point is developed in Figure 4. Consider two extreme forms of the relationship between male fitness (measured by survival of his offspring to fledging) and the level of male parental care. If a reduction of male care is compensated by the female, or other individuals, as in Dunnocks *Prunella modularis* (Burke et al. 1989), loss of male care does not negatively affect male fitness (line A). In that case, the male might adjust the level of his care in direct proportion to his confidence of paternity. However, if a reduction of male care is not compensated, and if the male cannot recognize his own offspring so that a reduction of his care to the nest has a negative effect on survival of his own as well as other nestlings, the male is predicted to provide full care regardless of his confidence of paternity until some threshold is reached, at which point he would stop providing care (line B). This threshold level might be higher if there are other mating options for the male (line B') (Whittingham et al., in prep). Since a reduction in male care in Tree Swallows is not compensated by the female (Leffelaar & Robertson 1986) or other individuals, and males cannot recognize and therefore feed only their own genetic offspring, this type of threshold relation rather than a linear decrease in male care as confidence of paternity declines probably holds for Tree Swallows. Given such a threshold response, female behaviour which influences male confidence of paternity, such as frequent or prolonged copulation, may maintain the male's confidence of paternity above the threshold and therefore prevent him from reducing his contribution to care of the offspring. In addition, it might prevent infanticide by males which have zero confidence of paternity.

This study demonstrates that strong competition for breeding opportunities, as occurs in many secondary cavity nesting species, has had an important influence in shaping the behaviour of male Tree Swallows, and probably females as well. Infanticide, or the threat of infanticide, may shape such behaviours as nest guarding (Møller 1988a), copulation, dispersal after nest failure, response to intruders and neighbours, and male-female interactions. This influence may be more widespread than has previously been recognized, and should be explored in other species.

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ENDOCRINE MECHANISMS AND THE EVOLUTION OF AVIAN PARENTAL CARE

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ABSTRACT. This paper reviews the endocrine mechanisms that accompany interspecific variability in avian parental behavior. Investigations of both domesticated and wild species have established a number of generalizations concerning the hormonal regulation of parental behavior. The rise and fall of circulating levels of the sex steroids just prior to the onset of incubation seems necessary for the transition from the sexual phase of the reproductive cycle to the parental phase in both males and females. The pituitary hormone prolactin is positively correlated with the occurrence of incubation behavior and has been implicated in both the induction and the maintenance of incubation. Studies of species that exhibit unusual patterns of parental care, such as brood parasites or sex-role reversed species; do not reveal major qualitative deviations from the endocrine profile reported for species exhibiting more common parental care patterns. It appears that major changes in behavior can occur with relatively minor endocrine changes. An understanding of the mechanisms that have accompanied the evolution of parental care diversity will require an elucidation of the relevant neural processes. Recent studies of interspecific differences in prolactin hormone receptors and intraspecific variation in the mechanism of sex steroid hormone action are reviewed in light of these findings.

Keywords: Testosterone, estradiol, prolactin, parental behavior.

INTRODUCTION

Parental care is a fundamental component of the life history of nearly all avian species. It appears to be a "primitive" life history characteristic that is a part of the group of morphological and behavioral adaptations that almost defines birds and differentiates them from their reptilian ancestors. Oviparity and endothermy make it essential that all eggs receive some sort of attention after oviposition, although it is not necessarily the case that the newly hatched young will require any attention from its parents (Oring 1982).

Diversification of the class Aves has included patterns of parental behavior. Biparental care of some sort is the primitive pattern and remains the most common (Lack 1968, Silver et al. 1985). But, the roles adopted by the sexes and the types of care provided the offspring vary greatly among taxa. All birds lay eggs that require attendance of some sort for successful hatching. The type of post-hatching care provided has co-evolved with the mode of development of the young. Altricial development is most common in the class Aves though it appears to be the derived condition, precocial development being the primitive condition (Ricklefs 1983). Altricial young are generally helpless at hatching and therefore must be brooded and fed by their parents. Precocial young are somewhat independent at hatching and may only require supervision by the parents.

Although parental care patterns have been described in detail (e.g. Nice 1962), rather less is known about the endocrine mechanisms that accompany this behavioral diversity. In this paper I will briefly review what is known about the hormonal control of parenting in birds and discuss the potential relevance of these endocrine mechanisms to an understanding of the evolution of avian parental care.

THE NEUROENDOCRINE SUBSTRATE MEDIATING PARENTAL BEHAVIOR

The hypothalamo-pituitary-gonadal axis

The major hormones that have been implicated in the onset and maintenance of parental care in birds are secreted by either the pituitary gland or the gonads. These critical endocrine glands are part of the major neuroendocrine "axis" that regulates nearly all aspects of reproduction, the hypothalamo-pituitary-gonadal axis. This system consists of the neurons in the hypothalamus that synthesize and release peptide hormones into the portal blood vessels that in turn regulate the production and release of pituitary hormones such as prolactin and the gonadotropins, luteinizing hormone and follicle-stimulating hormone. The gonadotropins regulate the gonadal steroids that feed back on hormone sensitive sites in the brain and/or the pituitary to regulate themselves by either positive or negative mechanisms.

These hormones have been implicated in the regulation of parental care either because changes in the secretion of these hormones are correlated with various parental activities and/or because manipulations of these hormones have prevented or modified various aspects of parental care. Correlational studies, especially when one considers feral species, are much more common than investigations that manipulate the hormones. I will first consider correlational and experimental studies in birds that show the most common avian reproductive behavior pattern, namely biparental care within a putatively monogamous mating system. I will then discuss species that show deviations from this pattern.

STUDIES THAT CORRELATE HORMONE LEVELS WITH BEHAVIOR

Generalized avian profile in biparental species

Based on studies of a variety of domesticated and feral species a generalized avian endocrine profile, illustrated in Figure 1, can be described that mediates the transitions from courtship behavior to nest building to incubation to the care of the young (Silver 1978, Wingfield & Farner 1980, Balthazart 1983, Goldsmith 1983, Wingfield et al. 1987, Silverin 1988, Gratto-Trevor et al. 1990). In both males and females gonadal steroids such as the estrogens, androgens, and progestins and the pituitary gonadotropins, luteinizing hormone and follicle stimulating hormone, tend to be high during the courtship and the nest building period regardless of the role played by either sex in nest-building (Figure 1). If either or both sexes engage in parental care the transition to incubation that occurs during egg laying involves a decline in the gonadal steroids and the gonadotropins and a rise in prolactin (see Wingfield & Farner 1980, Balthazart 1983 and Goldsmith 1983 for reviews).

One exception to this rule for the decline in sex steroids applies to progesterone in male birds, which in several species does not appear to change during the transition to incubation (e.g. Ball & Wingfield 1987, Silver et al. 1974) and in some cases even increases (Fivizzani et al. 1986). In species with polygynous mating systems such as the Red-winged Blackbird *Agelaius phoeniceus* where the male does not make the transition to incubation the decline in androgens is not observed (e.g. Beletsky et al. 1989). In most avian species, a rise in plasma levels of prolactin is correlated with the onset and maintenance of incubation behavior (see Goldsmith 1983 and Lea 1987 for reviews). If only one sex incubates, levels of prolactin in that sex are generally far higher than in the other during incubation (Goldsmith 1983, Gratto-Trevor et al. 1990).

GENERALIZED AVIAN HORMONE PROFILE

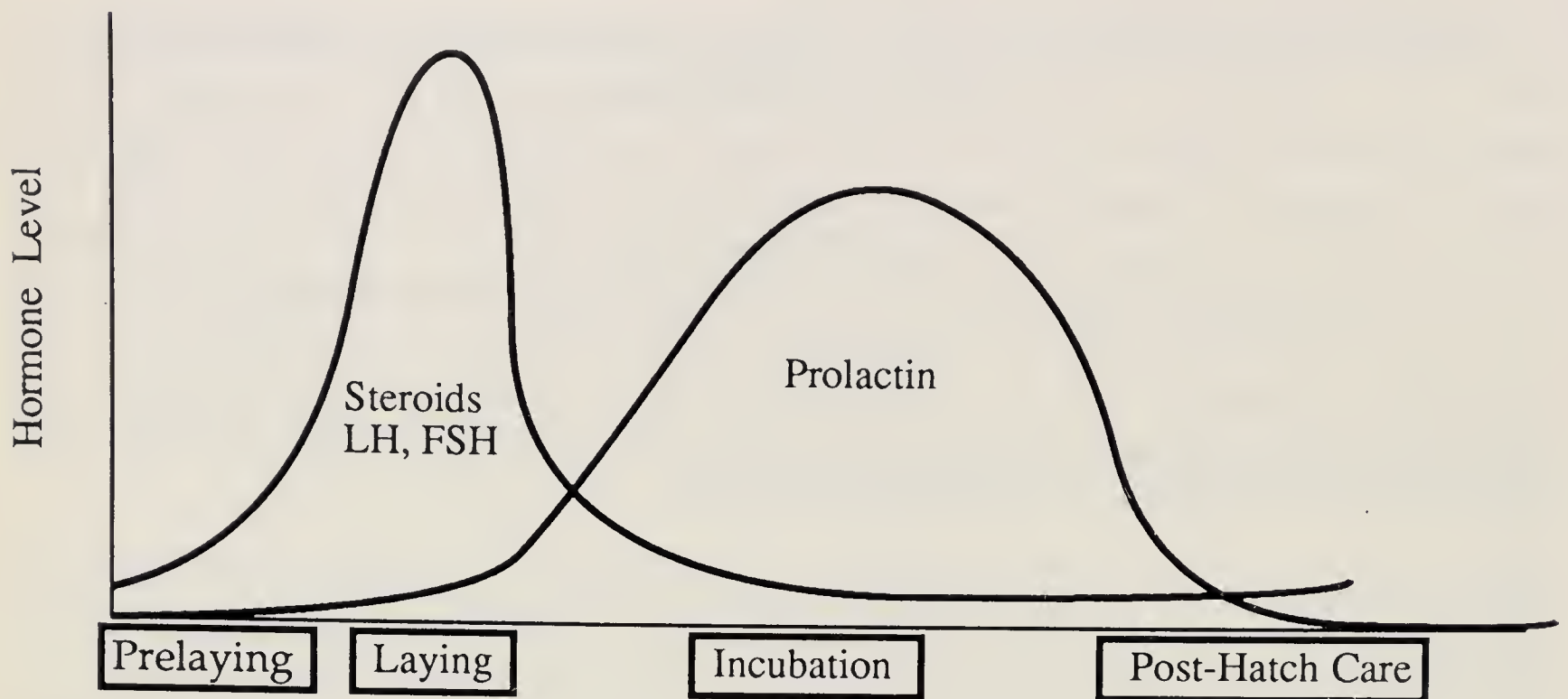


FIGURE 1 - Schematic diagram illustrating the generalized pattern of plasma hormone secretion derived from studies of avian species. Plasma levels of the sex steroid hormones, such as the androgens and the estrogens, as well as the pituitary gonadotropins such as luteinizing hormone (LH) and follicle-stimulating hormone (FSH), tend to be high during the prelaying and laying period. If the transition to incubation occurs it is usually associated with decline in plasma levels of these hormones and an increase in plasma prolactin levels.

However, this correlation between gonadal steroid decline and rising prolactin being associated with the onset of incubation is not always observed. For example, in apparently monogamous Passerines, males do not incubate or incubate very little (all members of the suborder Passeres lack brood patches). But, it has been shown in three songbird species, European Starling *Sturnus vulgaris*, White-crowned Sparrow *Zonotrichia leucophrys* and Song Sparrow *Melospiza melodia*, that testosterone (T) nonetheless declines just prior to incubation and prolactin rises during incubation. However, in every case the male prolactin levels are lower than those measured in females (Dawson & Goldsmith 1982, Hiatt et al. 1987, Wingfield & Goldsmith 1990). In these species as is true in most Passerines, these males subsequently feed their altricial nestlings after they hatch. In general, although there appears to be a good correlation between the combination of declining plasma levels of the sex steroids and the gonadotropins and rising prolactin levels with the onset of incubation, this correlation is clearer in females than in male birds.

Exceptions to the generalized pattern among biparental species

One well studied-exception to this pattern among biparental monogamous species occurs in the Columbiformes. As illustrated by the Ring Dove *Streptopelia risoria* both parents engage in parental care and both parents exhibit a decline in the plasma levels of the gonadal steroids prior to the onset of incubation (Silver 1978, Cheng 1979). However, as reviewed by Lea (1987), prolactin levels do not rise until incubation is under way (day 5 of a 14 day incubation period). This variant in the pattern of prolactin secretion is thought to be associated with the fact that Ring Doves, like all Columbiformes, possess a crop sac, in which they produce a milky substance fed to the young. This crop is well known to be prolactin dependent and it grows near the

end of incubation to insure that it is fully developed in time to feed the squab; it appears to be costly to develop the crop sac early in incubation.

EXPERIMENTAL STUDIES OF THE HORMONAL BASIS OF PARENTAL BEHAVIOR IN BIPARENTAL SPECIES

Studies that have investigated in detail the causal role these hormones play in the control of parental care using the standard methods of hormone removal and replacement have generally been limited to domesticated forms that breed in captivity such as the Ring Dove, Canary *Serinus canarius*, the Domestic Fowl *Gallus domesticus*, and Turkeys *Meleagris gallopavo*. It is beyond the scope of this communication to review in detail all the experimental work resulting from these studies and the reader is referred to the following reviews (Cheng 1979, Silver 1978, Balthazart 1983, Lea 1987, El Halawani et al. 1990). However, a few examples will be described. In female Ring Doves, estradiol and progesterone are essential for nest-building to occur and for the transition to incubation behavior (Cheng & Silver 1975). In female Turkeys it is clear that estradiol and progesterone acting in synergy with prolactin is essential for the onset of incubation (El Halawani et al. 1986) whereas in doves which possess an unusual pattern of prolactin secretion this hormone seems to be important for the maintenance but not the onset of incubation (Buntin 1986, Lea 1987). Males have been studied less intensively, but results for Ring Doves suggest that males are affected more by situational and stimulus factors than by endocrine physiology compared with the female (Silver 1978, Balthazart 1983).

Studies of non-domesticated species in the field have generally been limited to manipulating plasma levels of hormones by administering hormone implants. Most of this work has been done on males and it suggests that maintaining high T levels by implanting intact males with capsules containing the hormone is incompatible with parental care (Silverin 1980, Hegner & Wingfield 1987, Oring et al. 1989). Female European Starlings apparently also require a decline in the gonadal steroids, estradiol and progesterone, to fully maintain incubation (Ball & Wingfield 1986). These steroid implant studies suggest that the hormones are activating behaviors that are incompatible with parental care rather than directly inhibiting neural pathways mediating parental behavior.

Experimental studies of prolactin in nondomesticated species are rare because of the difficulty in manipulating this hormone that is secreted by the pituitary. Pedersen (1989) administered prolactin to intact free-living female Willow Ptarmigan *Lagopus lagopus* and found that there was no increase in incubation constancy but there was a slight increase in their sitting tightness and in their distraction display rate when flushed off the nest. As reviewed in the previous section of this paper, studies in feral birds that correlate hormone levels and parental care, in general, reveal hormone profiles consistent with the notion that prolactin acts synergistically with the sex steroids to stimulate the onset of incubation.

Declining prolactin levels have been related to the termination of the incubation of infertile eggs or to the termination of the brooding of the young in Ring Doves (Silver 1984). Silver (1984), however, found no evidence that prolactin was involved in the maintenance or termination of the parental feeding of the young in this species. Studies of free-living species such as the Semipalmated Sandpiper *Calidris pusilla* by Gratto-Trevor et al. (1990) and the Pied Flycatcher *Ficedula hypoleuca* by Silverin &

Goldsmith (1990) were both unable to find a relationship between plasma prolactin levels and the decline in brooding. Although, further study is necessary it is possible that the termination of parental care, unlike its onset, is mediated primarily by non-hormonal factors as has been argued to be the case in certain mammalian species (e.g. Reisbick et al. 1975).

HORMONAL STUDIES OF THE MAJOR BEHAVIORAL EXCEPTIONS TO THE GENERALIZED AVIAN PATTERN

Field endocrinologic investigations have been conducted on two groups that might be considered behavioral "exceptions" to the generic avian pattern. These are the brood parasitic Brown-headed Cowbirds *Molothrus ater* and the sex reversed polyandrous species such as the Spotted Sandpiper *Actitis macularia*, Wilson's Phalarope *Phalaropus tricolor*, and the Red-necked Phalarope *Phalaropus lobatus*. Somewhat surprisingly, studies of both these groups of birds have failed to reveal the major endocrine deviations that one might expect. Cowbirds possess a sex steroid hormone profile and a pattern of gonadotropin secretion over the course of the breeding cycle not unlike nesting species (see Dufty & Wingfield 1986 for a review). These brood parasites are essentially "locked" into the sexual phase of the nesting cycle and their endocrine profiles reflect this. However, they do show a seasonal pattern in prolactin secretion that is reminiscent of nesting species (Dufty et al. 1986). Similarly field endocrinologic investigations of the sex-role reversed species did not reveal a major reversal in the pattern of the gonadotropins or the gonadal steroids (Fivizzani et al. 1986, Oring et al. 1986a, Fivizzani & Oring 1986). The pattern of prolactin secretion in these species was also not anomalous. Although plasma levels of prolactin are higher in males than in females during the incubation and brooding periods this is to be expected since males, depending on the species, engage in either all or most of the incubation and brooding (Oring et al. 1986a, b, Gratto-Trevor et al. 1990). Thus major changes in the reproductive behavior of a species do not appear to be accompanied by a radical reorganization of endocrine secretions. Physiological factors influencing these behavioral differences should be sought in the neural sites that the hormones act on to activate behavior.

COMPARATIVE ANALYSIS OF BRAIN AREAS CONTAINING PROLACTIN RECEPTORS AND STEROID HORMONE RECEPTORS

Ball et al. (1988,1990) have compared the binding sites for prolactin in Brown-headed Cowbirds, Red-winged Blackbirds and European Starlings. Although the qualitative patterns are similar, quantitative differences have been found in the preoptic area with cowbirds showing substantially lower levels of binding than species exhibiting parental care. It is well known that this area is a central site mediating the hormonal onset of parental care in mammals and, to the degree it has been studied, in birds as well (Numan 1988, Komisaruk 1967, Erickson & Hutchison 1977, El Halawani et al. 1990). It is thus plausible that the failure of cowbirds to make the transition from the sexual phase of the breeding cycle to the parental phase has involved a change in central sensitivity to hormones and not a major change in the peripheral actions of the hormones themselves.

Balthazart & Ball (1990) have compared the biochemical actions of T in two steroid sensitive areas of the Japanese Quail *Coturnix coturnix japonica* brain. The

diencephalic preoptic medial nucleus (POM) is an important site mediating the actions of T on male copulatory behavior and the nucleus intercollicularis (ICo) is a midbrain site containing receptors for sex steroids that is involved in the regulation of vocal behavior. There are differences in these two areas in the number and type of steroid receptors that are present, in the amount and type of steroid metabolizing enzymes that can be detected in each nucleus, and in the nature and type of neurochemical change that is induced by T in the different areas. It is still impossible to relate these biochemical differences directly to the differential behavioral actions of T in these two nuclei but the comparison does illustrate how the same hormone acting in the same brain can have very different consequences depending on the nature of its target site. Similar differences may explain interspecific differences in hormone action (Silver & Ball 1989).

CONCLUSION

Based on the comparative studies reviewed above, there have been only slight adjustments of a basic hormone pattern mediating the evolution of parental care in birds. There is no evidence of a major constraint on the behavioral role adopted by either sex during parental care as occurs in mammals. For example, except for oviposition, male birds can exhibit the full range of parental behavior exhibited by females; in mammals, lactation is restricted to the female. The behavioral specializations of birds during parental care do not suggest major constraints on the evolution of new behavioral adaptations. However, we do not understand what the key physiological variables are that have permitted or mediated the evolution of these various ways of being parental (or not parental). For example, it seems to be a general phenomenon that within populations males exhibit greater variance in parental care than do females but we still need to establish the basis for variation in male response to a particular stimulus. One hint can probably be found in the fact that correlations between hormone changes and behavior are not as tight in male birds as in females. It should be remembered that hormones are not thought to directly induce a behavior but rather effect the probability and intensity of the behavioral response that an animal will give to a particular stimulus (Feder 1984, Moore & Marler 1988). What has happened in male birds that makes the linkage between hormonal secretion and behavioral response different from what is observed in females?

Are there any hormones that have not yet been considered that should be studied in relation to the induction of parental behavior in birds? The posterior pituitary peptide hormone, oxytocin, has been implicated in the regulation of maternal behavior in mammals (e.g. Pedersen & Prange 1979). Its avian form (mesotocin) has, to my knowledge, never been investigated in relation to parental care in any avian species. Perhaps this hormone has undergone extensive modification in its function in birds and is an important factor underlying species differences. However, up to the present time no hormone has been identified that mediates parental care in a specialized parental (or nonparental species) that has not been found to also be involved in the regulation in other more characteristic species. In other words, as has been observed many times before, the origin of behavioral specializations does not seem to involve new hormones but changes in the regulation of existing ones. The critical question at present for those interested in understanding the evolution of mechanisms mediating parental care is the identification of these regulatory changes (Silver & Ball 1989). One of the first steps that needs to be completed will be to elucidate the neural basis of the hormonal induction of parental behavior in any avian species. Once a model

species has been studied in detail one can then approach the problem of how behavioral variations have evolved.

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CONCLUDING REMARKS: PARENT-OFFSPRING INTERACTIONS IN THE EVOLUTION OF AVIAN LIFE HISTORIES

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ABSTRACT. Parental care and genetic relationship bind adult and offspring into a coadapted unit whose evolution depends on the environment-specific and taxon-specific outcomes of behavioural interactions between parent and offspring and between siblings. Among issues resolved by selection are the level and duration of parental provisioning of food and other care, and competition between offspring. Selection manifests itself in adjustments of brood size, care solicitation and response, development pattern and rate, synchrony of development within the brood, length of the breeding cycle, and the underlying behaviours and physiological processes required to realize these adaptations.

Keywords: Parental care, parent-offspring conflict, development, provisioning, hatching synchrony, sibling competition, life history, growth rate.

INTRODUCTION

Parental care is a conspicuous feature of the class Aves. The parental-care system, which includes contributions from both the parent and offspring, comprises three interconnected components: (a) parental modification of the immediate environment of the offspring, (b) offspring demand for food energy, nutrients, and heat, and (c) parental provisioning in response to demand. The system exists within the context of a distinctive environment for each population, and it is expressed in the various life-history attributes of the population.

ALTRICIAL AND PRECOICIAL DEVELOPMENT

The pattern of parental care depends on the conditions of the environment, the nature of the food resource of the population, and the mode of development of the offspring. Development in birds occupies a spectrum between the extremes of altricial (highly dependent) and precocial (generally independent) condition of the neonate (Portmann 1954, Nice 1962, Ricklefs 1983, Starck 1989). Position on this spectrum trades independence off against rate of development (Ricklefs 1979). To a greater degree than altricials, precocial chicks are endothermic and self-feeding, generally releasing the parent from food provisioning and brooding to undertake other activities, thereby increasing adult survival and fecundity. The price of precocial development is slow growth and prolonged vulnerability of the chicks to time-dependent mortality factors. Birds exhibit precocial modes of development when food supplies are accessible to small, non-volant chicks (e.g. Galliformes, Anseriformes) or when the exploitation of distant food supplies by the parents precludes extended brooding of the chick (e.g. Procellariiformes, some Charadriiformes). When parents must feed their offspring, altricial development permits rapid, energetically efficient growth.

PARENTAL MODIFICATION OF THE ENVIRONMENT

Parents ameliorate the environment of the chick by nest site selection (Calder 1973, Webb & King 1983, Clark et al. 1983, Nillson 1984), the construction of the nest (Schaefer 1980, Skowron & Kern 1980, Møller 1990), brooding behaviour (Clark & Ricklefs 1988), defence of the nest and chicks (Breitwisch 1988, Wiklund 1990, Hudson 1990), and food provisioning.

The parent forms a bridge between the offspring and its environment, often having to arrive at compromises between the requirements of the clutch or brood and the availability of resources in the environment. Nest site and construction are constrained by substrates and materials, yet must meet requirements for a suitable thermal environment and safety. Dietary requirements may be satisfied only by selective foraging.

Furthermore, the diet may change as the young grow and their need for particular macromolecules compared to energy declines. The distant feeding grounds of petrels require that adults transport meals enriched in energy ("stomach oils") (Place et al. 1989). Such energy-rich diets may be coevolved with slow postnatal development, which reduces the requirement for nutrients relative to energy (Ricklefs 1991a). Such diets also reduce the total water intake of the young and may thereby constrain the thermal environment space of the chick (Kirkley & Gessaman 1990), forcing small petrels, for example, to nest in cool, humid burrows rather than on the surface (Sievert & Ricklefs, in prep.).

Economics of temperature regulation in shorebirds dictate that it is more economical for small chicks to be brooded by the parent than to do their own thermoregulation (Chappell 1980). The maintenance of a high body temperature in the chick requires the production of excess body heat to replace that lost to the environment under most conditions. Even in precocial birds, the parents provide a part of this heat in the form of brooding, which decreases under warm conditions and with increasing age (Beintema & Visser 1989). The sharing of thermoregulatory costs represents the solution of an economic problem balancing the costs to each party in terms of the allocation of time and the income and expenditure of energy, within the constraints established by the physiology of the organism (Clark 1982, 1984, Clark & Ricklefs 1988). Among shorebirds, small species rely much more heavily on parental brooding than do large species, as is true of most groups (Dunn 1975), although in all shorebird species neonates can elevate metabolism to about twice resting, thermoneutral levels in response to cold stress (Visser & Ricklefs, in prep.). To maintain their body temperatures in the absence of brooding, neonates of small species would have to elevate heat production to over 10 times the resting metabolic rate, which may not be supportable by foraging (Beintema & Visser 1989) or food processing (Kirkwood 1983, Kirkwood & Webster 1984, Nir et al. 1978), or would greatly prolong development by increasing the precocity of the neonate.

FOOD SOLICITATION AND RESPONSE

To gain adequate nutrition, chicks must communicate their nutritional state and the parents must respond to solicitation appropriately (Henderson 1975, Bengtsson & Ryden 1981, 1983, Hussell 1988, this symposium). Within the limits of the parents' ability to acquire food, this system ensures that chicks grow properly. To the extent

that parents cannot fully satisfy the requirements of the brood, the intensity of food solicitation behaviour may also provide a basis for allocation of food among the brood (see Hussell, this symposium; Mock 1987, Anderson 1989, Drummond 1989).

When poor nutrition of the chicks increases intensity of solicitation, which in turn stimulates increased parental foraging effort, optimal brood size of the parents may be adjusted below the number of young that potentially can be reared, particularly if foraging effort were regulated by solicitation from the young rather than governed by some intrinsic criterion of the parent. In this situation, the demands of the chicks could literally work the parents to death physiologically or expose them to increasing hazards. Under varying and unpredictable resources, parents should adjust clutch size to the number they can rear in the poorest year so as not to jeopardize their own survival. Such a model may explain the inverse relationship between clutch size and survival independent of the breeding season, and also why so many brood enlargement experiments reveal that adults can rear additional offspring, presumably during good years.

Ricklefs (1987, 1991b) has argued that petrels lack solicitation response mechanisms owing to the long intervals between feeding (several days), independence of feeding by each parent, and highly variable meal size. Lacking information on the nutritional state of the chick, parents must establish an intrinsic rate of feeding. When rate of feeding varies and parents estimate the appropriate feeding level with error, they should overestimate. This may account for the accumulation of unusually large fat reserves in petrel chicks, which eventually must be burned off during a "starvation period" before the chick is light enough to fly (Ricklefs, unpubl.).

PARENT-OFFSPRING CONFLICT

Offspring have their own agenda which may differ from that of their parents, and which can lead to parent-offspring conflict over the allocation of care within the brood and the termination of parental care (Trivers 1974, Parker & Macnair 1978, Anderson & Ricklefs in review). One important area of conflict is over the rate of growth of the embryo and chick. When parents cannot provide sufficient food to adequately nourish the entire brood, the smallest (usually the youngest or least rapidly growing) chick is at greatest risk of death. As Werschkul & Jackson (1979) pointed out, under such circumstances sibling competition selects for rapid growth. But rapid growth also increases the daily food requirement of the brood and may further limit the fecundity of the parent. Slow postnatal growth in species that rear only one chick per brood suggests an energetic advantage, especially where risk of time-dependent mortality is low.

Sibling competition should also select for rapid embryonic development, but some groups of birds with multichick broods exhibit greatly prolonged incubation periods compared to others (e.g. Psittaciformes, Coraciiformes, some suboscine Passeriformes). In most such cases, hatching is totally asynchronous, and laying and hatching intervals frequently exceed one day (Ricklefs in prep.). When eggs hatch synchronously, initial rank in the competitive hierarchy is influenced by hatching time, hence by rate of embryonic growth. When parents commence incubation with the first egg in the clutch and eggs hatch asynchronously, the parent controls the competitive

hierarchy by its laying and incubation behaviour; rapid embryonic development is no longer selected because genetic variation in development rate cannot reverse the parentally imposed competitive ranking. Under these circumstances, factors favouring slower development exert relatively more influence.

Parent and offspring may also conflict over the termination of parental care (weaning). Offspring always personally gain from continued parental care, although at a rate that diminishes with age as the chick can better care for itself. From the parent's point of view, the optimum age at weaning depends on the relative fitness value of its contribution to older young compared to a fresh set of eggs. These values are determined by the degree to which the parent can increase the survival of the egg or chick, but also by the schedules of mortality independent of parental care (Ricklefs 1969). Thus, when nest predation is very high, fledged young are relatively more valuable to the parent than a new clutch of vulnerable eggs, and fitness may be increased by extending the period of parental care. Ricklefs (1969) argued that these considerations may explain the generally prolonged periods of parental care in tropical birds, although difficulty of obtaining food resources may also be a contributing factor.

ADAPTIVE RESPONSIVENESS OF THE PARENT-OFFSPRING SYSTEM

To what degree are adaptive responses in the parent-offspring system restricted by considerations of physiology and taxonomic relationship? The answer to this question may be found in analyses of taxonomic levels of variation. The separation of nest building and egg laying in obligate brood parasites and facultative, intraspecific brood parasites suggests a general evolutionary independence of several categories of breeding behaviour. In one species of swift, the female lays a second egg after the first chick has hatched, suggesting that egg-laying and chick-feeding are not behaviourally or hormonally incompatible (Tarburton & Minot 1987). *Eudyptes* penguins lay two eggs of markedly different size in each clutch, and preferentially incubate the second, larger egg so that it hatches first (Williams 1981). Although such traits as clutch size and rate of postnatal development appear to be extremely flexible, with considerable diversity exhibited at low taxonomic level, others appear more highly constrained. Viviparity may be precluded by the high body temperature of birds (Anderson et al. 1987). Pattern of development within the altricial-precocial spectrum generally varies only among taxonomic orders, and rarely among families (Nice 1962, Ricklefs 1983). Incubation period also is conservative, with most of the variation, after normalization for egg mass, being attributable to differences among taxonomic orders. The general conservatism of some aspects of development (and related aspects of parental care) are strikingly illustrated by species of Procellariiformes (semiprecocial) and Pelecaniformes (altricial) nesting side-by-side from the Antarctic to the Equator.

INTRAPOPULATION VARIATION

In contrast to the conservatism of some attributes of the life history, others, particularly behavioural traits, exhibit considerable variation within populations. Examples have been provided in this symposium regarding parental feeding (Boersma, Gowaty), foraging response (Hussell), and confidence of paternity (Robertson). Many others will

readily come to mind. This variation not only challenges our understanding of the contextual contingencies of behavioural response, but also provides opportunities for experimental tests of ideas relating parent and offspring behaviour to components of evolutionary fitness.

CONCLUSIONS

The parent-offspring system is a coevolved unit whose properties reflect the conditions of the environment, the requirements of the developing offspring (including influences of sibling competition on these requirements), and the direct interaction between the parent and offspring. As yet, this system is poorly known, in spite of the wealth of observational data on avian life histories and behaviour. The criteria by which the system is optimized can be understood in terms of economic models of time and resource allocation between parent and offspring and demands on time and resources imposed by the environment and competition between offspring. As some of the examples presented above suggest, observed life-history patterns may be influenced by the nature of the solicitation-response behavioural system that couples parent and offspring. In particular, if parental response is insensitive to perceived parental risk, reproductive effort can be controlled only by clutch or brood size. Furthermore, multiparous broods establish selection for rapid development that may reduce the parent's fecundity, and thus create parent-offspring conflict. Finally, the responsiveness of the parent-offspring system is constrained by certain morphological and physiological considerations that preclude the existence of some phenotypes. Most of these factors are amenable to comparative, experimental, and modeling analyses. The parent-offspring system of birds provides excellent opportunities for studying the evolution of complex systems, integrated by behavioural interactions within the family group, and placed in a wide diversity of environmental settings.

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SYMPOSIUM 15

BROOD PARASITISM

Conveners M. PETRIE and A. P. MØLLER

SYMPOSIUM 15

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INTRODUCTORY REMARKS: BROOD PARASITISM

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Intraspecific nest parasitism occurs whenever females lay eggs in the nests of conspecifics without caring for the offspring. Although intraspecific brood parasitism was first described in birds, an increasing number of studies have documented its occurrence in insects with parental care (e.g. Tallamy 1985).

Intraspecific brood parasitism has been studied relatively less intensively than interspecific brood parasitism. Nest parasitism of conspecifics was largely neglected until Yom-Tov (1980) drew attention to its causes and evolutionary consequences in an important review article. Since then an increasing number of studies have reported its occurrence in a diverse array of bird species ranging from altricial to precocial birds. Brood parasitism has been discovered by direct observation but also, more recently, by biochemical methods of assigning maternity using the techniques of gel electrophoresis and DNA-fingerprinting. In this symposium, Eadie shows that nest parasitism occurs throughout the Anatidae family and is not a feature of a particular tribe or genus. It appears that nest parasitism is much more common than was previously supposed.

At the time of Yom-Tov's review the most commonly cited cause of nest parasitism was some sort of nesting failure and it was thought that females parasitised the nest of others because they had lost their own nests or failed to acquire suitable nest sites. Since then more detailed studies have suggested that nest parasitism is an alternative reproductive tactic which can be adopted by females which also have nests of their own. As a strategy nest parasitism by females is equivalent to males seeking extra-pair copulations in pair-bonded species, since, in both cases, individuals can benefit from parasitising the parental care of conspecifics by avoiding the time and energy costs of raising offspring. This view is amply supported by the contributors of this symposium: Pinxten, Lyon and Eadie all find that a certain amount of parasitism can be attributed to females which also have nests of their own in Starlings, American Coots and Goldeneyes, respectively. Furthermore, Lyon shows that parasites are producing extra eggs to lay parasitically.

If nest parasitism is a reproductive strategy favoured when the costs of rearing young outweigh the costs of producing eggs it could be predicted that all individuals, in egg-laying species with parental care, could be susceptible to nest parasitism and should take steps to try to prevent it. Possible host anti-parasite tactics are considered in this symposium by Pinxten and in the paper by Møller and Petrie. Pinxten shows that Starlings can remove the eggs of parasites under some circumstances and considers whether the time birds start their clutches is affected by the risk of parasitism in

populations of Starlings. Møller and Petrie suggest that producing characteristically patterned eggs that vary little within a clutch may be a means by which hosts can recognise whether or not they have been parasitised.

The 'arms race' (sensu Dawkins & Krebs 1978) that results between hosts and parasites *within* a species has only rarely attracted the attention of theoreticians (but see Andersson 1984), and in this symposium May looks at how the existence of brood parasitism within a species can be evolutionarily stable. He also predicts how antiparasite behaviour will result in population cycles.

The most fundamental questions arising from this symposium concern the costs of reproduction and in particular the relative costs of producing eggs or rearing offspring. Without real estimates of these the fitness consequences of acting as a nest parasite or a host cannot be finally evaluated.

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BROOD PARASITISM IN EUROPEAN STARLINGS: HOST AND PARASITE ADAPTATIONS

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ABSTRACT. In this report, we review brood parasitism in the European Starling *Sturnus vulgaris*, a semi-colonially breeding hole-nesting passerine, focusing on parasite and anti-parasite behaviour. The reported frequencies of brood parasitism in well-studied populations ranged from 5 to 30%. The possible identity of parasitic females is discussed. Parasites adopt tactics which seem to increase the success of parasitism: (1) They usually lay their eggs synchronously with the host's laying sequence. (2) They occasionally remove one of the host's eggs prior to depositing an egg of their own. (3) They usually lay only a single parasite egg in a host's nest. (4) They probably actively search for unattended nests. Nesting birds appear to use some tactics to minimize the cost of parasitism, like (1) active removal of parasite eggs deposited prior to the time when they, themselves, initiate egg laying, and (2) laying a smaller clutch as a form of 'insurance' against the crowding effects of brood parasitism.

Keywords: European Starling, *Sturnus vulgaris*, intraspecific brood parasitism, host adaptations, parasite adaptations, egg removal.

INTRODUCTION

Until recently, most researchers studying intraspecific brood parasitism have focused mainly on documenting the presence of the phenomenon. In most species where intraspecific brood parasitism is known to occur, the effects of brood parasitism on the reproductive success of both host and parasite have not been thoroughly explored empirically (but see Gibbons 1986, Emlen & Wrege 1986, Møller 1987, Brown & Brown 1989). Also, compared with interspecific brood parasitism, relatively little work considers the evolutionary consequences of parasitism on both host and parasite behaviour (but see Møller 1987, Brown & Brown 1989, Gowaty et al. 1989).

Intraspecific brood parasitism has been relatively well studied in several populations of the European Starling¹ *Sturnus vulgaris*, a semi-colonially breeding, hole-nesting passerine. In this paper, we review the available information on intraspecific brood parasitism in the European Starling. We briefly discuss the possible identity of parasitic females in this species and then we focus on parasite behaviour and on possible host defences against brood parasitism.

FREQUENCY AND PATTERNS OF OCCURRENCE

Reports of brood parasitism in the Starling have been both anecdotal (Yom-Tov et al. 1974, Power et al. 1981, Feare 1984) and well documented (Karlsson 1983, Evans 1988, Lombardo et al. 1989, Romagnano et al. 1990, Pinxten et al. 1991). Table 1

¹ Common and scientific names follow Voous (1977)

TABLE 1 - Parasitism rates among first, intermediate and second clutches in several European Starling colonies. % percentage of parasitized nests (data from all years studied combined), values in parentheses indicate the range of yearly frequencies. N total number of nests. * ^{(1), (2), (3), (4), (5), (6), (7), (8)} refer to the criteria used to identify parasite eggs: (1) each newly added egg was marked individually with an alcohol-based pen on the day of laying; (2) the appearance of more than one egg/day before the host completed its clutch; (3) the appearance of eggs after the host completed its clutch; (4) unusual egg shape/size/pigmentation; (5) biochemical genetic markers; (6) one or more eggs disappeared from the nest; (7) eggs have been found beneath the nest; (8) direct observation; ** solitary nestboxes.

Study site and methods	First		Intermediate		Second		Total		Reference
	%	N	%	N	%	N	%	N	
Sjötorp, Sweden ^(2,6,7) *							5	270	Karlsson 1983
							(0-20)		
Revinge**, Sweden ^(2,6,7)							30	141	Karlsson 1983
							(7-44)		
Aberdeen, Great Britain ^(1,2,3,4,5)	27	95	15	20			25	115	Evans 1988
	(16-36)								
Surrey, Great Britain ^(1,2,3,4,5)	21	95	10	31	12	16	17	142	Evans 1988
	(11-37)								
New Jersey, North America ^(1,2,5)	23	138	1	91	4	55	12	284	Lombardo et al. 1989
New Jersey, North America ^(1,2,3)	26	111	5	75	6	55	15	241	Romagnano et al. 1990
	(14-36)								
New Jersey, North America ^(1,2,3,5)	28	72	11	27	5	19	20	118	Romagnano et al. 1990
	(8-37)								
Kalmthout, Belgium ^(1,2,3)	6	34	0	10			5	44	Pinxten et al. 1991
	(0-9)								
Zoersel, Belgium ^(1,2,3,8)	16	50	4	55			10	105	Pinxten et al. 1991
	(0-37)								
Wilrijk, Belgium ^(1,2,3,8)	18	90	0	21			14	111	Pinxten et al. 1991
	(0-22)								

summarizes the parasitism rates reported in the well-documented studies measured as the proportion of clutches containing 'foreign' eggs, and the methods that were used to identify brood parasitism in each study. It is important to note that the estimated levels of parasitism must be regarded as minimal since some instances of brood parasitism may have gone undetected with the methods used (for more details, see Evans 1988, Romagnano et al. 1989, Romagnano et al. 1990, Pinxten et al. 1991). Table 1 clearly shows that intraspecific brood parasitism is a widespread phenomenon in most of the well-studied populations, with frequencies ranging from 5 to 30%. In each colony, the highly synchronously laid first clutches were found to experience the greatest rate of parasitism with dramatic declines in rates for intermediate and second clutches (Table 1). In all studies, the proportion of parasitized first clutches usually varied between years (Table 1).

IDENTITY OF PARASITIC FEMALES

The identity of parasitic Starling females was only rarely determined, but there is some indication that certain ecological factors can affect the rate of parasitism and these data suggest which females may be acting as parasites. Nest site availability (or at least availability of good nest sites) seems to be an important factor determining the incidence of nest parasitism in Starlings. Karlsson (1983) found that nest parasitism occurred only when all nestboxes were occupied and Evans (1988) reported that parasitism rate among first clutches increased with the relative occupancy of nestboxes between years and areas. These results suggest that parasitic females may be mainly (paired) females without access to suitable nest sites (see Karlsson 1983, Evans 1988). However, Pinxten et al. (1991) recently showed that a shortage of (suitable) nest sites may not be the only selective pressure underlying brood parasitism in Starlings. Unlike Karlsson (1983) and Evans (1988), they described and analysed the frequency of nest parasitism in nestbox colonies with a low nestbox occupancy (36% - 78%). They found that the rate of parasitism amongst first clutches, in most years, was very high (up to 37%; see Table 1), despite an excess of available unoccupied suitable nestboxes, and that parasitism rate was not positively related to nestbox occupancy. These findings indicate that brood parasitism in the Starling can occur even when there is an excess of good nest sites.

Evans (1988) found that parasitism rates among first clutches increased with an increase in the rate of first clutch desertions of unparasitized nests. He suggested that paired Starling females which lose or desert partially completed clutches may also act as parasites in his study site. This suggestion was supported in another study by the direct observation of a colour-marked female Starling dumping an egg in the clutch of a neighbouring female, after deserting her nest due to disturbance, shortly before clutch initiation (see Pinxten et al. 1991). Because of semi-colonial breeding and the highly synchronized laying period during the first brood in Starlings (Karlsson 1983, Pinxten et al. 1990), a female whose breeding attempt is interrupted has the opportunity of recouping at least part of her reproductive success since large numbers of potential host nests in the correct stage are available. Emlen & Wrege (1986) showed that White-fronted Bee-eaters *Merops bullockoides* whose breeding has been interrupted will also parasitize the nests of other females.

Evans (1988) and Romagnano et al. (1990) both suggested that some parasitic Starlings might be unmated (generally young) females, fertilized by a paired male and with no nest of their own. This possibility is difficult to test. However, Pinxten et al. (1991) provided some circumstantial evidence to suggest that such females may be important parasites in colonies with a female-biased sex ratio during the first brood laying period.

Evans (1988) also suggested that some parasitic Starling females might be ‘mixed strategists’ (sensu Trivers 1972) which simultaneously tend their own clutch and parasitize other nests, as do parasitic Barn Swallows *Hirundo rustica* (Møller 1987), Cliff Swallows *Hirundo pyrrhonota* (Brown & Brown 1989) and Moorhens *Gallinula chloropus* (Gibbons 1986), or ‘pure parasites’ who lay all their eggs in other nests. However, Yom-Tov (1980) calculated that due to the high synchrony of laying in the Starling, it would not be beneficial for a female to become a pure parasite. Moreover, no pure parasites have been documented in any other species known to practise intraspecific brood parasitism. So far, there is also no direct evidence for the existence of mixed strategists in the Starling. However, a mixed strategy might be possible in the Starling because of the highly synchronized, colonial breeding. Extensive and continuous observations of colour-marked females in a colony, coupled with DNA fingerprinting techniques, are needed to further test this suggestion. However, on the basis of the available present information, nest parasitism in Starlings appears limited to an opportunistic, phenotypically flexible strategy used by females only when their own breeding is interrupted or when they have no access to nestboxes (see Pinxten et al. 1991).

PARASITE BEHAVIOUR

For parasitism to be a successful strategy a parasite egg must have a high probability of producing a fledgling (Hamilton & Orians 1965). Parasitic female Starlings appear to use several tactics which would increase the success of their parasitic egg-laying attempts.

TABLE 2 - Laying tactics of parasitic females in several Starling populations.

- ^a percentage (%) and number (N) of parasitized nests that were parasitized during laying;
- ^b percentage (%) and number (N) of parasitized nests receiving a single parasite egg;
- ^c percentage (%) and number (N) of parasite eggs occurring singly in a nest;
- * percentage or number of parasite eggs laid during the host’s laying period.

Study site	PL ^a		PSE ^b		PES ^c		Reference
	%	N	%	N	%	N	
Aberdeen, Great Britain	31*	9*	57	17	31	17	Evans 1988
Surrey, Great Britain	64*	16*	92	23	85	23	Evans 1988
New Jersey, North America			72	23			Lombardo et al. 1989
New Jersey, North America	64	23	95	106	85	45	Romagnano et al. 1990
Kalmthout + Zoersel + Wilrijk, Belgium	92	24	85	22	72	23	Pinxten et al. 1991

Starling parasites tend to lay their eggs during the host's own laying sequence (see Table 2) when brood parasitism is most likely to be successful and when host nests are most vulnerable to parasitism. Offspring from parasite eggs laid during the host's own laying period were found to have a significantly higher fledging success than those from eggs laid after its completion. The latter usually never fledged (Yom-Tov et al. 1974, Evans 1988, Romagnano et al. 1990, Pinxten et al. 1991). Parasitic White-fronted Bee-eaters also lay their eggs synchronously with their hosts and spend many hours observing the nesting activities of potential hosts (Emlen & Wrege 1986). In contrast, Moorhens are relatively poor parasites in that they lay their eggs at random during the host's laying and incubation period. As Starlings begin incubating before clutch completion (Meijer 1990), eggs laid at the end of the host's laying sequence hatch later and produce runts which have a low chance of fledging relative to eggs which hatch earlier (Litovich 1982 *in* Lombardo et al. 1989). This suggests a selection pressure on parasites to lay early during the host's laying sequence. Accordingly, Lombardo et al. (1989) and Romagnano et al. (1990) reported that most (77% and 84%) parasitic eggs laid before the host completed its clutch were laid during the first three days of the host's laying sequence (modal clutch size was five eggs in both studies). However, Pinxten et al. (1991) found that parasitic eggs laid during the host's laying sequence were evenly distributed over a six day laying cycle.

Most parasitized Starling nests receive only single parasite eggs (Table 2). This may indicate that parasites usually lay only a single egg in each of several host nests. If a parasite spreads her eggs over several nests, her young may be raised in smaller broods than if she lays in only one host nest (Andersson 1984). Scattered laying is therefore favourable in the Starling where offspring mortality seems to increase with brood size (Lack 1948, Tinbergen 1981, Westerterp et al. 1982). Accordingly, Evans (1988) found that the number of parasitic young fledged per egg laid was highest when a smaller number of parasite eggs were added to a nest. Alternatively, the observed pattern of egg dumping may indicate that most parasitic females lay only one parasitic egg.

Several investigators have suggested that parasitic female Starlings (Yom-Tov 1980, Karlsson 1983, Feare 1984) possibly behave like some cuckoos which remove an egg from the host's nest before laying their own (Payne 1977). Lombardo et al. (1989) examined the association between egg removal and brood parasitism in the Starling and found a chronological and statistical association between these two phenomena. Egg removal occurred significantly more often at nests where brood parasitism was detected than at unparasitized nests, as was also reported by Evans (1988) and Pinxten et al. (1991). The sequence of events at nests where egg removal and parasitism were both detected suggests that parasites indeed sometimes remove host eggs at the nests they parasitize (Lombardo et al. 1989, Pinxten et al. 1991). The alternative explanation, that egg removal was the result of hosts removing parasite eggs that they discover in their nests (Evans 1988) could be excluded since Starling hosts appear to be unable to discriminate between their own and parasite eggs once they, themselves, begin egg-laying (Karlsson 1983, Stouffer et al. 1987, Pinxten 1989). This indirect evidence of egg removal by parasites was confirmed by two direct observations of a parasitic female removing an egg while parasitizing a nest (Pinxten et al. 1991).

Feare et al. (1982) reported that some parasites laid later in the day than the peak period of laying when hosts are less likely to be present and able to evict the intruder

(see also Romagnano et al. 1990). Also, Starling parasites seem to be able to lay their eggs remarkably quickly (R. Pinxten, M. Eens, personal observation), which minimizes the time spent at the nest thereby reducing the chances of being detected.

Parasitic female Starlings thus exhibit several behaviours that suggest adaptive fine tuning. In general, however, it appears that most parasitic females will be much less successful at producing offspring than if they were to lay in nests of their own, assuming that they lay the same number of eggs and that they were not themselves parasitized (Evans 1988, Romagnano et al. 1990, Pinxten et al. 1991). However, if the alternative to parasitism was total reproductive failure (see above), a parasitic strategy would be favoured (Romagnano et al. 1990). So far, the potential long-term benefits of brood parasitism such as the possibility of increased survival as a result of not having to rear young (Andersson 1984) have not been addressed in the Starling.

CONSEQUENCES OF PARASITISM FOR THE HOST

There are two main ways in which nest parasitism may reduce the host's fitness relative to that of unparasitized female Starlings. Firstly, parasitic Starling females sometimes remove one of the host's eggs before laying their own. Lombardo et al. (1989) and Pinxten et al. (1991) found that removal of one or more of the host's eggs occurred at 34% and 27% of parasitized nests, respectively. Secondly, addition of one or more hatchlings may reduce the number of host's offspring fledged because of increased competition within the enlarged brood (Crossner 1977, Tinbergen 1981), and it also may reduce the survival of the host because of the increased costs of parental care (Clobert et al. 1987). Pinxten et al. (1991) found that at least 41% of parasitized females raised one extra hatchling. Romagnano et al. (1990) reported that fewer host's young fledged from parasitized than from nonparasitized clutches. In general, parasitized nests had a significantly larger clutch size than normal nests, but fledged significantly fewer young (Evans 1988, Pinxten et al. 1991).

ANTI-PARASITE BEHAVIOUR

As brood parasitism may depress host fitness in Starlings, one may expect selection to favour behavioural traits that reduce the risk or costs of being parasitized. The most common host adaptation against interspecific brood parasites is egg rejection (Rothstein 1975). Experimental parasitism (Stouffer et al. 1987, Pinxten 1989) revealed that Starling hosts are able to recognize and remove parasite eggs, but only before clutch initiation. A similar lack of discrimination against parasite eggs after clutch initiation has been documented in several other species (Brown 1984, Emlen & Wrege 1986, Møller 1987, Brown & Brown 1989).

Another anti-parasite behaviour is nest guarding. In White-fronted Bee-eaters (Emlen & Wrege 1986), Barn Swallows (Møller 1987), Cliff Swallows (Brown & Brown 1989) and Eastern Bluebirds (Gowaty et al. 1989), hosts reduce the risk of being parasitized by guarding their nests. However, in Starlings, nests are commonly left unguarded early in the laying period, during which they mainly forage on communal feeding grounds away from the nest (Feare 1984). As male Starlings need less food than the laying female, they could defend the nest while the female is away foraging. However,

male Starlings accompany their female away from the nest early in the laying period in order to prevent cuckoldry (Power et al. 1981, Pinxten et al. 1987, Eens & Pinxten 1990), thereby leaving their nest exposed to parasitism. Power et al. (1981) suggested that cuckoldry may pose a greater threat to males than brood parasitism since usually only single parasite eggs are found in nests, whereas a single extra-pair copulation potentially can fertilize several eggs.

Yom-Tov (1975) suggested that synchrony of egg laying may be a defence mechanism against nest parasitism. An individual that lays during the peak of synchrony may, theoretically, have a lower chance of being parasitized, since there are a greater number of potential host nests. But, in all well-studied Starling populations first clutches experienced the highest rate of parasitism (Table 1) and these were laid highly synchronously. Therefore, it seems unlikely that laying synchrony in the Starling evolved mainly as a defence against conspecific brood parasitism (see Karlsson 1983).

Starlings thus do not seem to have evolved any well-developed behaviours to avoid being parasitized. Apart from nest-guarding, lack of defensive behaviours against conspecific nest parasitism seems to be a general pattern in all species studied so far (see Brown & Brown 1989 for references). A possible host adaptation which could reduce the costs of being parasitized is to stop laying when the total clutch reaches normal size, as do parasitized Goldeneyes *Bucephala clangula* (Andersson & Erickson 1982). Karlsson (1983) and Power et al. (1989) concluded that Starlings are determinate layers and do not adjust their laying to the number of eggs in the nests. However, Meijer (1990) recently provided circumstantial evidence that Starlings might act as indeterminate layers before the third egg is laid. Power et al. (1989) suggested that hosts in their population laid fewer eggs than they could successfully rear in an apparent attempt to avoid the costs of raising an oversized brood in the event of parasitism. This 'Parasitism Insurance Hypothesis' should be applicable only for those populations where the frequency of brood parasitism is high enough for birds to forsake an optimal clutch size all the time (see Power et al. 1989). However, Rothstein (1990) questioned the validity of this hypothesis.

CONCLUSIONS

We can conclude that, although brood parasitism has been relatively well studied in several Starling populations, the identity of parasites and the detailed tactics of parasites and hosts still remain to be clarified. Extensive and continuous observations of colour-marked females within a colony for several years, coupled with DNA-fingerprinting techniques, are still needed to determine the identity, status and laying tactics of parasitic female Starlings and to obtain more accurate measures of the reproductive success and survival of parasites and hosts in this species.

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COULD INTRASPECIFIC BROOD PARASITISM CAUSE POPULATION CYCLES?

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ABSTRACT. Building on earlier work by Andersson and others, we first show that among birds where the costs of raising a chick are significantly greater than those of successfully laying an egg, the strategy of laying some or all eggs in others' nests can result in enhanced reproductive success. The consequent evolutionary trajectories can have the perverse outcome that the ESS is one where average reproductive success is substantially lower than in the parasite-free population; at the ESS, optimal clutch size may be significantly larger or smaller than in the absence of parasitism, depending on the biological details. All this produces strong pressures to evolve vigilant behaviour, which in turn can lead to cycles in population density (within naive populations, parasitism increases in frequency; within highly parasitized populations, vigilance pays; within mainly vigilant and thus parasite-free populations, naive birds increase in frequency by avoiding the costs associated with vigilance; and so the cycle starts again). In this preliminary report, we sketch some deliberately simplified models that illustrate these ideas about how intraspecific brood parasitism can affect overall population dynamics.

INTRODUCTION

For altricial birds, the costs of raising a chick result in there being — in some average sense — an optimal clutch size that is usually significantly less than the number of eggs that could be produced. In this situation, a parasitic member of the population that successfully laid some or all of its eggs in others' nests could in many circumstances have greater reproductive success than its fellows. The ensuing evolutionary trajectories can, depending on the behavioural and ecological details, lead to evolutionary stable states (ESS) in which average clutch sizes are smaller or larger than in the naive population, and where average reproductive success within the population is substantially lower than that prevailing before parasitism appeared. The situation is akin to the well-analysed economic phenomenon whereby a sole owner can manage a resource to maximise sustainable profit, but where the "economic rent is dissipated" in the absence of sole ownership (Clark 1976). Hardin has popularized these ideas as the "tragedy of the commons".

As a consequence, there are strong pressures for birds to evolve vigilant behaviour of various kinds — nest guarding, egg inspection, synchronous breeding, and others (Andersson 1984, Møller 1989) — to reduce the chance that a nest will be parasitized by other members of their population. Such vigilance has costs, measured in time or energy that could otherwise be channelled toward enhancing reproductive efforts. At the level of the overall dynamics of the population, the outcome can be cycles in population density: the frequency of parasitism rises among populations of naive birds; the frequency of vigilant birds thus increases; this is followed by the frequency of naivety then rising among a largely parasite-free population of vigilant birds (because of the costs of vigilance); and so back to the start of the cycle.

Previous studies of intraspecific brood parasitism have not, to our knowledge, given thought to the implications for the overall dynamics of the population. The models presented below are deliberately oversimplified.

Their aim is to make plain the basic ideas sketched above. Many refinements, specific to particular situations, will be needed before such models can make detailed contact with field studies of individual bird species. Some such refinements are indicated below.

BROOD PARASITISM AND ESS CLUTCH SIZE

Andersson (1984) has given a good account of the evolutionary dynamics of intraspecific brood parasitism (IBP) at the level of individual nests. In particular, he considers optimal clutch sizes under the assumption that the density-dependent relation between number of eggs laid, x , and number of fledglings raised, $F(x)$, has a logistic form:

$$F(x) = x [1 - ax] \quad (1)$$

In the absence of brood parasitism, the optimal clutch size, n_o , is

$$n_o = 1/2a \quad (2)$$

and the reproductive success is $F(n_o) = 1/4a$.

Now suppose the nest is parasitized by a parasite that produces y additional eggs in the nest. Assuming that the fledging success of the host is now $F(x) = x [1 - a(x + y)]$, Andersson shows that the host's optimal clutch size is now reduced to $n_o = \hat{n}_o (1 - ay)$, and that the corresponding reproductive success is now $\hat{F}(\hat{n}_o) = (1 - ay)^2/4a$. This corresponds to the host producing half an egg less for each one laid by the parasite (but still having to raise a larger brood).

Andersson, however, did not give explicit consideration to the relative reproductive success of the parasite. If the host behaves optimally, the parasite has $F(y) = (1/2) y (1 - ay)$. Thus, even if the parasite only lays eggs in one nest (and it could often do more than this), it will have greater reproductive success than the host provided $F(y) > \hat{F}(\hat{n}_o)$. This condition is fulfilled if $y > 1/3a$, which is to say if

$$y > (2/3) n_o \quad (3)$$

Here n_o is, as above, the parasite-free optimal clutch size. This criterion, eq (3), should not be too hard for a parasite to fulfil.

More specifically, if the parasite also behaves optimally it will lay $y_o = 1/2a$ eggs in the host nest, for a reproductive success of $F(y_o) = 1/8a$. In this event, the host's reproductive success is $\hat{F}(\hat{n}_o) = 1/16a$, or one half that of the parasite.

In short, once the parasitic trait has appeared, it is likely to spread fast (in the absence of one or other form of vigilant behaviour by the host). The exact details of the ensuing ESS will depend on the details of the assumptions we make, but all such ESSs will

tend to result in each member of the population having lower reproductive success than prevailed in the pristine, parasite-free, population.

We outline one particular model which is broadly representative of a wider class of models for ESSs in the absence of vigilance.

Once the parasitic habit has been fully established within the community, we assume each bird lays a total of n eggs (with n possibly significantly larger than n_0 , because it is much cheaper to produce eggs than to raise them). Of these n eggs, x are first placed in the individual bird's own nest, and then the remaining y are placed in other birds' nests. Each time a parasitic egg is dumped in a nest, one of the existing eggs is removed, so that clutch size remains constant at x . The density-dependent fledging success function is assumed to decrease exponentially with increasing clutch size, as $\exp(-\alpha x)$, (rather than linearly like $(1 - \alpha x)$, as in the calculations of Andersson and above). Finally, we assume that, all other things being equal, a parasitic egg has a fledging success rate that is lower, by a factor γ ($\gamma < 1$), than that of a host egg (to allow for inappropriate timing of incubation, etc.).

With these assumptions, the first question is what is the probability, $g(n, x)$, that an egg originally laid in one's own nest will remain, and not be ejected by a parasite? This probability can be shown to be

$$g(n, x) = \exp(-y/x) = \exp(1 - n/x) \quad (4)$$

The overall reproductive success of a typical member of this population is then

$$F(n, x) = [xe^{-y/x} + \gamma x (1 - e^{-y/x})] e^{-\alpha x} \quad (5)$$

Here the first term inside the square brackets represents eggs laid in one's own nest, reduced by the probability of surviving ejection. The second term represents the average outcome for eggs laid in others' nests, discounted by the factor γ . The factor $\exp(-\alpha x)$ represents the usual density-dependent effects. From eq (5) we see that, if n is significantly larger than x (so that y/x is largish), most of the reproductive success comes from parasitic eggs, even though each has an intrinsic discount factor of γ .

For specific values of the parameters n, α , and γ , the ESS-value of x , x^* say, can be found in the standard way, as that value such that a bird departing from it (by laying fewer (or more) eggs in its own nest, and correspondingly more (or fewer) parasitic eggs) will do worse than the others. The resulting ESS-value of x is given by the equation

$$\beta = \frac{1}{s^2} - \frac{\gamma}{1-s} \left[\exp\left(\frac{1}{s} - 1\right) - 1 \right] \quad (6)$$

Here we have, for notational convenience, defined $s = x^*/n$ (so that $1 > s > 0$). We have also written $\beta = n/n_0 = \alpha n$, where n_0 is the optimal clutch size in the absence of parasites ($n_0 = 1/\alpha$); β is thus the ratio between the number of eggs now laid by each bird, n , and the parasite-free optimum number ($\beta > 1$).

Explicit analysis of eq (6) is straightforward but messy. Since we are aiming to paint a broad picture, a few limiting results are sufficient to make our main points.

First, we observe that in the limit of small γ (hatching success of parasitic eggs heavily discounted), eq (6) has the solution $s \approx \beta^{-1/2}$. That is, the clutch size in this limit ($\gamma \rightarrow 0$) is

$$x^* \approx (n/n_o)^{1/2} n_o \quad (7)$$

This is larger than the parasite-free optimum, n_o , and can be a lot larger if $n \gg n_o$. For larger values of γ , however, it can be that few own-nest eggs escape ejection, leading to an ESS where nearly all eggs are laid in other nests; in this event, it can easily happen that x^* falls below n_o . For example, suppose $\beta = 1.2$ (total number of eggs 20% above the parasite-free optimum) and $\gamma = 0.81$: then the ESS clutch size is $x^* = 0.6n_o$ (60% of the parasite-free optimum value).

Second, we note that the ESS reproductive success, obtained by substituting the solution of eq (6) into eq (5), is always less than that for parasite-free birds. Specifically, in the limit of small γ , the ratio between the ESS reproductive success and the reproductive success of parasite-free birds is roughly $\beta^{1/2} \exp(2 - 2\beta^{1/2})$; this ratio can be quite small if β is large (that is, number of eggs laid significantly larger than the optimal clutch number in the absence of parasites). When the discount factor for parasitic egg success, γ , is not so small, the ratio between ESS and parasite-free reproductive successes can get close to unity, although always remaining below it. For the numerical example cited above ($\beta = 1.2$, $\gamma = 0.81$) the ratio is 0.79.

As emphasised above, this particular model is representative of a wide class of such models. The essential message is that, once the parasitic habit has appeared in the population, it is likely to spread, eventually leading to mixed strategies where the average number of chicks fledged under the ESS is lower — sometimes much lower — than in the pristine, parasite-free community. The clutch size in typical nests under the ESS may be larger, or it may be smaller, than the parasite-free optimal clutch size, depending on the details of the biological assumptions and parameter values.

POPULATION DYNAMICS AND BROOD PARASITISM

Up to this point, we have been developing a theme familiar to economists. A sole owner — a bird dealing with its own nest and fledglings in the absence of parasitism — can evolve behaviour (such as an optimal clutch size) that maximises the returns on its efforts. But in a “commons” exploiters will continue to enter the market — parasites will tend to lay eggs in others’ nests — until the point is reached where the marginal rate of return is zero (profits balance costs); everyone loses, locked into the perverse, and sometimes tragic, logic of the commons. In economic terms, the solution is to construct regulatory mechanisms that effectively restore sole ownership, for sustainably profitable management. In terms of IBP, the solution is to evolve one or other form of vigilant behaviour, to prevent parasitism and recover “sole ownership” of the nest.

As Andersson (1984) and others have noted, such vigilance will have costs, and the upshot is likely to be some polymorphism in which parasitic behaviour persists, albeit at relatively low frequencies (if parasitism disappeared completely, then vigilance, with

its attendant costs, would in turn be lost, and so on). Such frequency-dependent situations are more fully appreciated, and more fully analysed, in the context of hosts and viral, bacterial, protozoan or helminth parasites (Hamilton 1980, May & Anderson 1983; see also May & Robinson 1985, for a discussion of these issues in relation to interspecific brood parasitism).

What is less appreciated is that such polymorphisms do not necessarily have a stable form, but rather can lead to cycles in the proportions of the population adopting the various strategies, and even to cycles in the overall population size. We now illustrate how this can happen, using a grotesquely oversimplified model to make the basic mechanism clear. We then indicate how a variety of realistic refinements can be grafted onto this basic model.

Suppose our population consists of three types of birds: vigilant, naive, and parasitic. Our most extreme assumption, which will be reviewed later, is that this population has discrete, non-overlapping generations; each year the adults fledge their young and then die, while the fledglings go on to become next year's adults. We label the total populations of vigilant, naive, and parasitic birds in generation t as V_t , N_t , and P_t , respectively.

Vigilant and naive birds lay clutches of n_1 and n_2 eggs, respectively. As discussed above, we follow Andersson (1984) in assuming logistic density-dependent effects on fledgling success, so that the reproductive successes of vigilant and naive birds, in the absence of parasites, are respectively

$$F_v = n_1 (1 - a_1 n_1) \quad (8a)$$

$$F_N = n_2 (1 - a_2 n_2) \quad (8b)$$

The costs of vigilant behaviour are described by assuming that $a_1 > a_2$. More precisely, the factor f , defined by

$$f = a_2/a_1 < 1 \quad (9)$$

measures the costs of vigilance. From eq (8), we see that without parasites the optimal clutch sizes for vigilant and naive birds, respectively, are $n_{1,0} = 1/2a_1$ and $n_{2,0} = 1/2a_2$, resulting in reproductive successes of $F_v(\text{opt}) = 1/4a_1$ and $F_N(\text{opt}) = 1/4a_2$. Under these assumptions, we observe that $F_v(\text{opt})/F_N(\text{opt}) = f$, which is less than unity (thus measuring the costs of vigilance when parasitism is absent).

Now suppose a population of P_t brood parasites are present in generation t . We assume each parasite attempts to lay κ eggs in each of λ nests (not discriminating between vigilant and naive nests), with each parasite egg being discounted by the same factor, γ , that we discussed above. Each time a parasite egg is successfully deposited, one of the existing eggs is removed from the nest, so that the clutch size in naive nests remains at n_2 . The vigilant birds are assumed to be so efficient as to be immune from parasitism, so that their reproductive success remains fixed at $F_v(\text{opt}) = 1/4a_1$. The naive birds, on the other hand, suffer parasitism, with the result that in generation t only a proportion g_t of their eggs survive the risk of being ejected by a parasite; the reproductive success of naive birds in this situation is $F_N(\text{opt}) = (1/4a_2)$

g_t . The remaining fraction, $1-g_t$, of eggs in naive nests (discounted by the factor γ) lead to the next generation of parasites, with a reproductive success of $F_p = (\gamma/4a_2)(1-g_t)$ from each naive nest.

Finally, we assume that other ecological factors limit the number of nests (vigilant plus naive) to a total of K in each generation, and that fledging success rates are sufficiently high to produce more than enough birds to use all the nest sites in each generation (no matter how high the levels of parasitism among naive birds). That is, we assume that, in each generation t

$$V_t + N_t = K = \text{constant} \quad (10)$$

The number of nests occupied by vigilant and by naive birds, respectively, are in proportion to the numbers of such birds successfully fledged in the previous generation. It thus follows, from the above discussion, that

$$N_{t+1} = \frac{KN_t g_t / 4a_2}{N_t g_t / 4a_2 + V_t / 4a_1} \quad (11)$$

Recalling the definition $f = a_2/a_1$ of eq (9) and the constraint $V_t = K - N_t$ of eq (10), we can rewrite eq (11) as

$$N_{t+1} = \frac{KN_t g_t}{N_t g_t + (K - N_t)f} \quad (12)$$

It remains to obtain an explicit formula for g_t , the probability that a naive bird's egg will escape being ejected from the nest by a parasite. If the average naive nest in generation t is visited μ_t times by parasites, ejecting κ eggs (replaced by their own κ eggs) each time, then g_t can be shown to be $g_t = \exp(-\mu_t \kappa / n_2)$. Recalling that n_2 has the optimal value $1/2a_2$, and noting that $\mu_t = \lambda P_t / K$ (P_t parasites each making λ visits to nests, distributed randomly among the total of K nests), we have

$$g_t = \exp(-2a_2 \kappa \lambda P_t / K) \quad (13)$$

But, from the discussion above, the number of parasites in generation t is given in terms of the number of naive nests in the previous generation by

$$P_t = (\gamma / 4a_2)(1 - g_{t-1}) N_{t-1} \quad (14)$$

Thus eq (13) can be rewritten as

$$g_{t+1} = \exp[-\Gamma (1 - g_t) N_t / K] \quad (15)$$

Here Γ represents the combination of parameters $\Gamma = \gamma \kappa \lambda / 2$.

With this simple and biologically sensible model thus defined and formulated, we have a pair of first-order difference equations, eqs (12) and (15), for the two variables N_t

and g_t . The other two dynamical variables, V_t and P_t , follow from eq (10) and from eq (14), respectively. We have a closed system of equations, whose dynamical behaviour can be studied by numerical simulations or analytically.

The essential dynamical properties of these overall populations of vigilant, naive, and parasitic birds are as follows.

First, the population dynamics depends only on the two parameters f (measuring the costs of vigilance) and Γ (measuring the egg-laying activity, and thence the impact, of brood parasites). The third parameter, K , in eqs (12) and (15) serves only to set the scale of the population sizes; we may measure N_t and V_t in units of K or, equivalently, we may put $K = 1$.

Second, three qualitatively distinct regimes of dynamical behaviour can now be distinguished. We label these (i), (ii), and (iii).

Case (i): $\Gamma < 1$. Here the reproductive capacity of the brood parasite is too low for it to be able to establish itself. The population thus consists purely of naive birds, at the constant density $N^* = K$.

Case (ii): $[\ln (1/f)] / [1 - f] > \Gamma > 1$. Here the parasite can establish itself, but the cost of vigilance is too high in relation to the modest levels of parasitism so that vigilance does not pay. The population consists of a constant population of naive birds, again at $N^* = K$, along with a constant population of brood parasites whose magnitude is given by eq (14) with $N^* = K$ and g^* from the implicit relation $g^* = \exp [-\Gamma (1 - g^*)]$.

Case (iii): $\Gamma > [\ln (1/f)] / [1 - f]$. Now the impact of parasitism in relation to the cost of vigilance is sufficiently large that subpopulations of vigilant birds can appear. All three strategies — vigilance, naivety, parasitism — can now co-occur. They may do so at stable levels (as is generally recognised) or in proportions that vary cyclically over time (which is not so widely appreciated). Specifically, two subclasses may be distinguished.

Case (iiia): There is stable co-occurrence if

$$\frac{\ln (1/f)}{1 - [1 - f] / [\ln (1/f)]} > \Gamma > \frac{\ln (1/f)}{1 - f} \quad (16)$$

The steady equilibrium values of the different subpopulations are given by $N^* = (K/\Gamma)(\ln (1/f))/(1 - f)$, $V^* = K - N^*$, and P^* from eq (14) with $g^* = f$. Note that the expression on the extreme left-hand side of eq (16) is always greater than that on the extreme right (for all $f < 1$).

Case (iiib): If parasitic activity is sufficiently high in relation to the costs of vigilance,

$$\Gamma > \frac{\ln (1/f)}{1 - [1 - f] / [\ln (1/f)]} \quad (17)$$

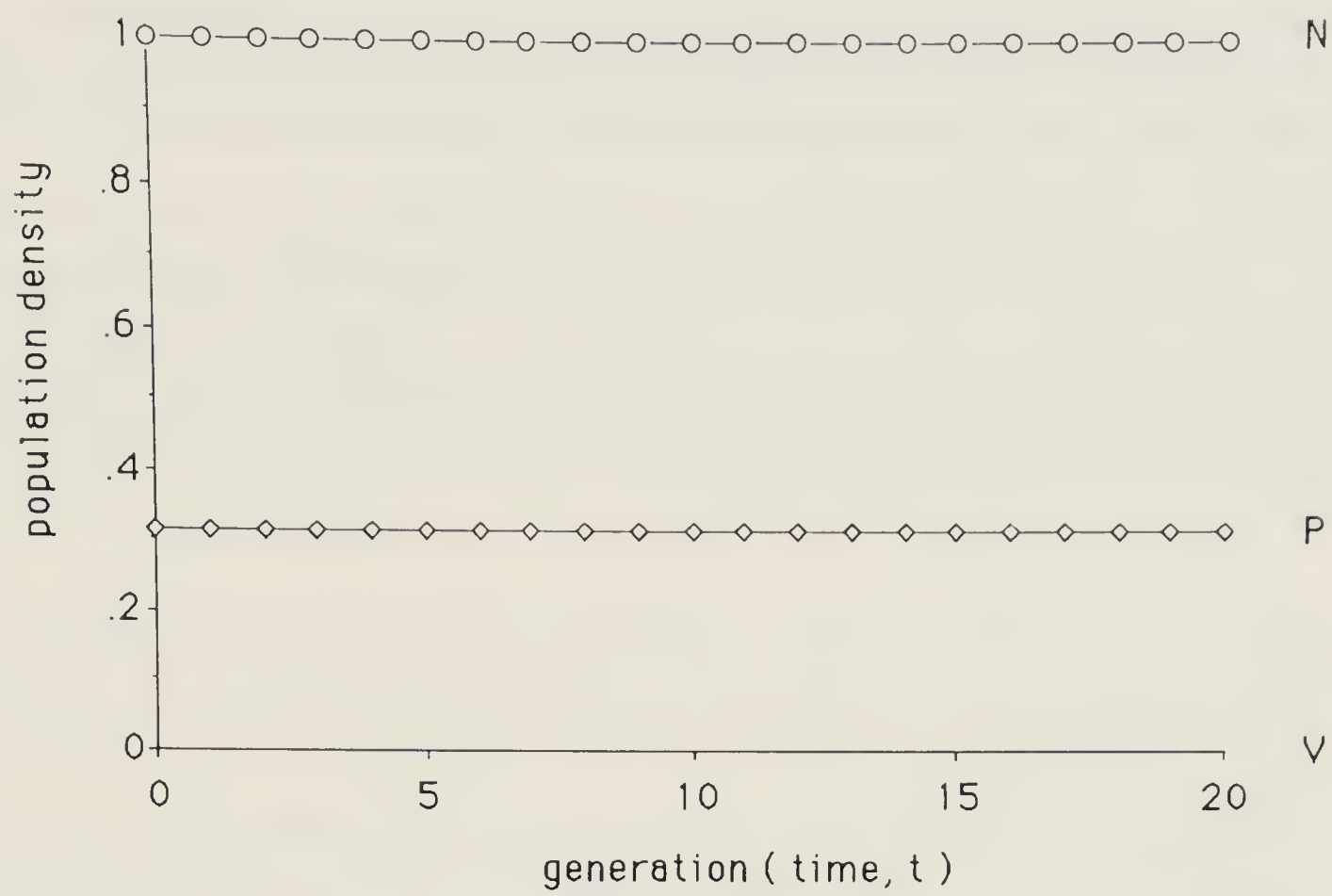


FIGURE 1 – This figure illustrates the long-term dynamical behaviour of the interactive system of vigilant, naive, and parasitic birds (with population densities denoted by V, N, and P, respectively) described by eqs (10), (12), (14) and (15). Here the parameter values lie in the range corresponding to “case (ii)”; specifically, $f = 0.5$, $\Gamma = 1.2$, and the scaling parameters have the arbitrary values $K = 1$ and $\gamma/4a_2 = 1$. In this case, the cost of vigilance is relatively high, and the population comprises only naive and parasitic birds.

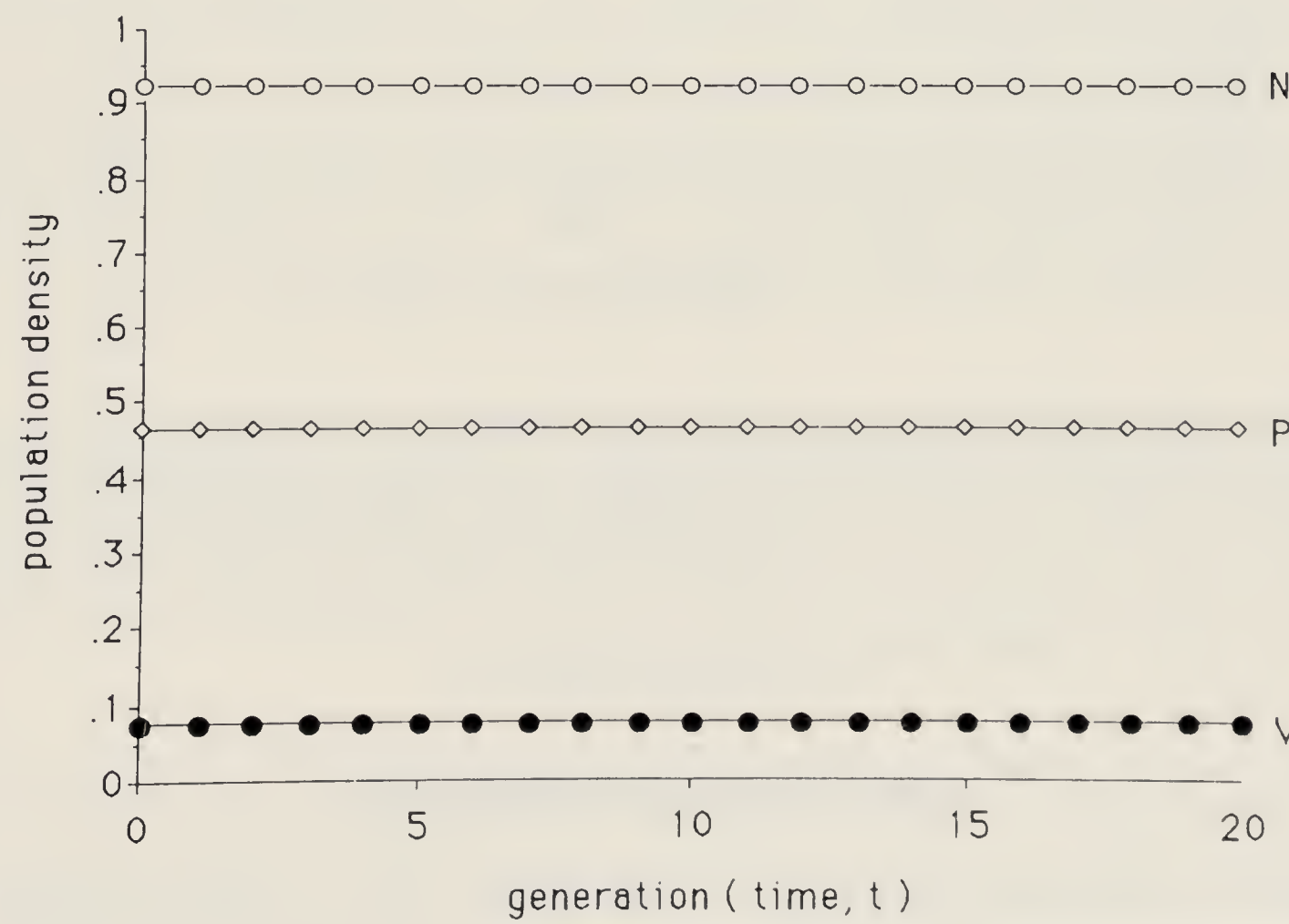


FIGURE 2 – As for Figure 1, but with $f = 0.5$ and $\Gamma = 1.5$. We now have “case (iiia)”, with all three subpopulations (V, N, and P) co-occurring at steady levels.

then all three subpopulations co-occur in proportions that oscillate in regular cycles. Although the total $N_t + V_t$ is constrained to remain constant at K , the fact that P_t oscillates means that the overall total population exhibits cyclic behaviour. That is, IBP can be a cause of population cycles.

This range of behaviour is illustrated in Figures 1-3. Figure 1 is a representative example of case (ii) (with $f = 0.5$, $\Gamma = 1.2$, and $\gamma/4a_2 = 1$ in eq (14)). Figure 2 depicts the stable co-occurrence of case (iiia) (here with $f = 0.5$ and $\Gamma = 1.5$), while Figure 3 shows the cyclic behaviour of case (iiib) (with $f = 0.5$ and $\Gamma = 2.5$). In Figure 3 the total population, $N + V + P$, also clearly cycles.

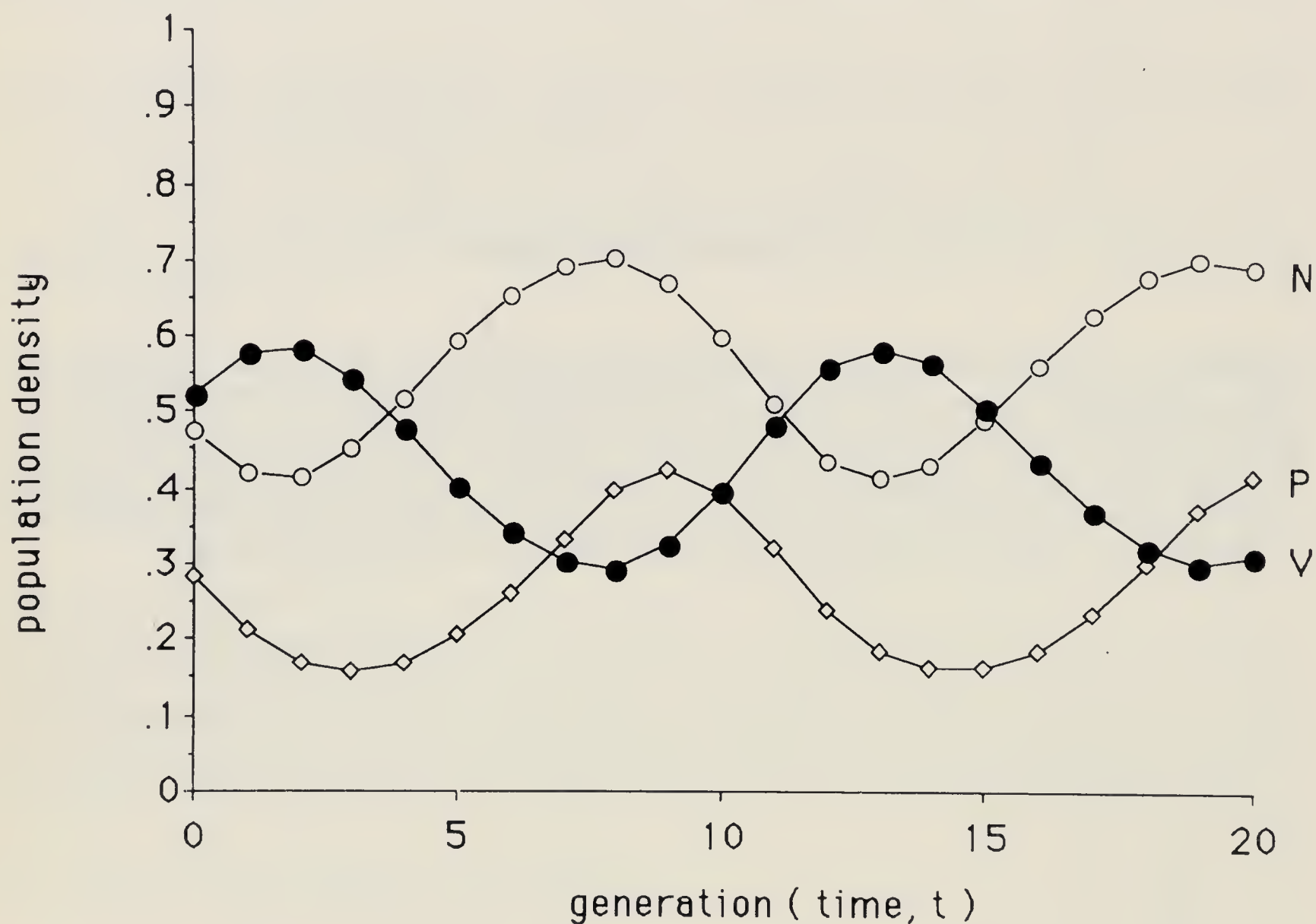


FIGURE 3 – Again as for Figure 1, but now $f = 0.5$ and $\Gamma = 2.5$. In this “case (iiib)”, N , V , and P all co-occur, but in proportions that settle to a pattern of sustained oscillations. In this simplest model, N and V are always exactly out of phase (N peaks when V is at a minimum), and in the usual way the parasites’ peak lags that of their naive hosts by a generation or two. As discussed in the text, not only do the populations cycle, but also the overall population exhibits cycles in total abundance.

SOME POSSIBLE REFINEMENTS

Our simple model assumed a fixed number of nest sites in each generation, with fledging success always sufficient to occupy them all (effectively we assume $a_2 K < 1$). The first thing to do is to relax this assumption, so that some sites remain empty at those points in the cycle where parasitism peaks. More generally, the overall

number of nest sites can be taken to be density-dependent (which can happen, for example, if territories contract at high density). Such modifications tend to make it easier for cycles to arise and to enhance the magnitude of their oscillation.

Most parasites add eggs without removal. Models with this feature are broadly similar to those above, and the tendency to cycle may be more pronounced.

More realistic models should include a fully age-structured treatment of the population, replacing the discrete, non-overlapping generations with many overlapping age classes. This will tend to make it more difficult for oscillations to arise, although they still will if Γ is big enough.

Our model is based on “types” or “strategies” among subpopulations. A more accurate, though more elaborate, analysis should deal with the population genetics of systems like this, representing the various strategies in terms of genotypes.

Furthermore, even within the simple framework presented above, it would be interesting to explore models in which individual birds pursued mixed strategies, combining parasitism with vigilance, say. It would also be more realistic for the vigilant birds not to be absolutely immune from parasitism, but rather to suffer diminished levels of IBP.

We believe, however, that our very simple model exhibits many of the basic features that IBP can produce at the population level.

CONCLUSIONS

The mechanism whereby IBP can result in population cycles is a robust one, reminiscent of the game of “scissors/paper/stone”. “Scissors cut paper”: parasites invade naive populations; “paper covers stone”: vigilant birds drive out parasites; “stone breaks scissors”: the cost of vigilance can be such that naive birds invade parasite-free populations of vigilant birds. Whether these inherent propensities will lead to sustained oscillations or will damp to steady polymorphisms depends on the interplay among the relevant parameters. But the potential for population cycles to be driven by IBP is there.

We hope that this work will stimulate field investigators to lift their sights above the behaviour of individual birds, and to consider the implications that such behaviour holds for the overall dynamics of the population.

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BROOD PARASITISM IN AMERICAN COOTS: AVOIDING THE CONSTRAINTS OF PARENTAL CARE

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ABSTRACT. Intraspecific brood parasitism was a common feature in a population of American Coots studied in central British Columbia, Canada. Depending on site and year, between 21% and 46% of the nests were parasitized, and 11% of all eggs over the three years of study were laid parasitically. Female coots laid eggs in the nests of other females in three different circumstances: (i) some parasitism was attributed to females without territories, (ii) a few females parasitized their neighbours after they lost their own nests to predators during laying, but (iii) most parasites were territorial, nesting females that laid one or more eggs in the nests of neighbouring pairs before initiating their own clutches. For territorial females with nests of their own, parasitism is an alternative reproductive tactic which allows them to overcome the constraints of parental care and thereby increase their total production of offspring.

Keywords: American Coot, *Fulica americana*, brood parasitism, parental care, indeterminate layers, British Columbia.

INTRODUCTION

Intraspecific brood parasitism (IBP) has now been reported in over 100 species of birds (Yom-Tov 1980, Rohwer & Freeman 1989), representing a diversity of taxa, social organizations, and patterns of parental care. Despite its widespread occurrence, the adaptive significance of IBP is poorly understood, largely due to the difficulties in identifying parasitic females (Andersson 1984). It is important, however, to identify parasites and their egg-laying tactics if we are to elucidate the evolutionary tradeoffs involved in laying eggs parasitically and test among alternative hypotheses for the adaptive basis of IBP.

To date few studies have been able to investigate IBP at this level of detail. So far, most studies have simply documented the occurrence of parasitism, but a few have also explored the consequences of parasitism to host success (e.g. Evans 1988) or examined adaptive host responses (e.g. Andersson & Eriksson 1982). The identities and laying tactics of parasites are known for only a handful of species, and most of these studies were unable to fully examine the evolutionary tradeoffs of parasitism and, therefore, provide a convincing explanation for why parasitism occurs.

I report here the results of a three year study of IBP in American Coots *Fulica americana* breeding in central British Columbia, Canada. I used variation in egg features among females to identify parasites, determine their laying tactics, and examine the tradeoffs involved in laying eggs parasitically.

STUDY ANIMAL, STUDY AREA, AND METHODS

I studied coots at three wetland sites: Beecher Prairie at Riske Creek in 1987 (84 pairs on 12 ponds in 1987); Jaimeson Meadow near Big Creek in 1988 and 1989 (52 and 43 pairs respectively on one large pond); Chilco West marshes near Hanceville in 1989 (129 pairs on 3 large ponds). Coots are monogamous in central British Columbia and the sexes share in incubation, feeding offspring, and defending the territory. They are single brooded but will renest up to three times if their clutch is destroyed by a predator. The chicks are semi-precocial and, although they leave the nest within a day or two of hatching, are fed by the parents on the territory for at least two weeks after hatching.

Almost all nests were found on the first or second day of laying and were monitored daily (228 nests) or every other day (80 nests) until hatch. I used two standard criteria (Yom-Tov 1980) to determine when parasitism occurred: (1) two or more eggs laid on the same day and (2) new eggs appearing after the host had ceased laying. Egg features (shape, spot pattern, background colour) vary considerably among females but little within a female's clutch (unpublished data). By visually comparing eggs in the field I was able to identify parasitic females that also had nests of their own, and to determine which of the eggs in hosts' clutches were laid by parasites, a technique used in other studies of IBP (Gibbons 1986, Møller 1987). In a few cases, egg features alone were used as a criterion that parasitism had occurred.

I followed the fates of parasite and parental eggs at nests by numbering all eggs, as they appeared, with an indelible felt pen. I marked chicks on hatch day with nape tags (Munro & Bedard 1977) containing a unique combination of two colored plastic beads. I monitored chick survival from floating blinds. Unbiased data on the survival of eggs laid by parasites are available for only 1989 so I limit my analysis of fecundity tradeoffs to that year.

IDENTITY OF PARASITES AND THEIR LAYING TACTICS

Parasitism was common in all three years and at all sites—from 21 to 46% of nests were parasitized each year (Table 1). Overall, 357 (11.4%) of the 3142 eggs in the study population were laid parasitically. Most parasitism was by paired, territorial females that also had nests of their own. Over the three years of this study 72 territorial females were identified as parasites and, depending on the year, these females comprised from 18 to 33% of the territorial females in the population (Table 1). Of the 357 eggs that were laid parasitically, 70% were attributed to territorial females. An additional 3 % were thought to have been laid by territorial females, but visual comparison of eggs for confirmation wasn't possible due to nest predation. The remaining 98 parasitic eggs include many known to have been laid by non-territorial females, identified by their unique egg characteristics, and the rest suspected of having been laid by non-territorial females.

Normally, females laid between one and 10 parasitic eggs and usually prior to initiating their own clutches. Seven females laid parasitically after their own partially complete clutches were destroyed by a predator.

TABLE 1 - Frequency of parasitized nests and territorial females that laid eggs parasitically each year.

Year	Nesting pairs	Parasitized nests (%)	Territorial parasitic females (%)
1987	84	18 (21.4)	15 (17.9)
1988	52	24 (46.1)	17 (32.7)
1989	172	73 (42.4)	40 (23.3)
Overall	308	115 (37.3)	72 (23.4)

TRADEOFFS IN FECUNDITY AND EGG SUCCESS

Most parasitism was by territorial females with nests of their own. To understand what these females gain from parasitism, we need to examine the tradeoffs they are making relative to nonparasitic territorial birds. ‘Clutch size’, for both non-parasites and parasites, is the number of eggs a female laid in her own nest, and includes only eggs in nests that successfully reached clutch completion. Clutch size decreased with laying date in the study population (Figure 1) so I used analysis of covariance to compare clutch sizes in parasites' own nests with the clutch sizes of nonparasites in 1989. The slopes for parasites and non-parasites did not differ ($F_{1,142} = 0.347$, $P = 0.57$), and clutch sizes of parasites and non-parasites did not differ when seasonal trends were controlled for ($F_{1,143} = 0.176$, $P = 0.68$; adjusted mean for parasites $7.9 \pm .25$ (36), for non-parasites $8.0 \pm .14$ (111)). Comparing the total number of eggs laid by parasites (clutch size in own nest plus eggs laid parasitically) with the clutch size of non-parasites indicates that parasites laid more total eggs than non-parasites. For this comparison the slopes for parasites and non-parasites differed, so a t-test was used to compare mean clutch sizes without taking seasonal trends into account; $t = 7.90$, $P < 0.0001$, 1-tailed test; $x_{\text{par}} = 11.54 \pm .58$ (35), $x_{\text{non}} = 8.16 \pm .16$ (111). These comparisons demonstrate that parasites are not laying parasitic eggs at the expense of their parental clutch size, but are producing extra eggs to lay parasitically. This finding is illustrated graphically in Figure 1 for one of the two wetland sites studied in 1989, the Chilco West marshes .

Eggs laid parasitically by territorial females were only 27% as successful at producing fledged young as parental eggs, considering parental eggs laid by both parasites and non-parasites (Table 2; comparison of successful and unsuccessful parental versus parasitic eggs, $G_{\text{adj}} = 41.5$, $P < 0.001$). However, parasites may have differed from non-parasites in their abilities as parents or in the quality of their territories, so it is also appropriate to compare the success of eggs that parasites laid parasitically versus in their own nests. Eggs laid parasitically were also much less successful than the eggs parasites laid in their own nests (24%, Table 2; $G_{\text{adj}} = 38.6$, $P < 0.001$).

Eggs laid parasitically were less successful for two reasons. First, many were laid late in the hosts’ laying cycles, when they had a low chance of fledging because of age-dependent brood reduction, or after the host had ceased laying, when they had virtually no chance of even hatching. Second, egg rejection behaviour is well developed in American Coots (unpublished data) and hosts rejected many parasite eggs that would have otherwise hatched.

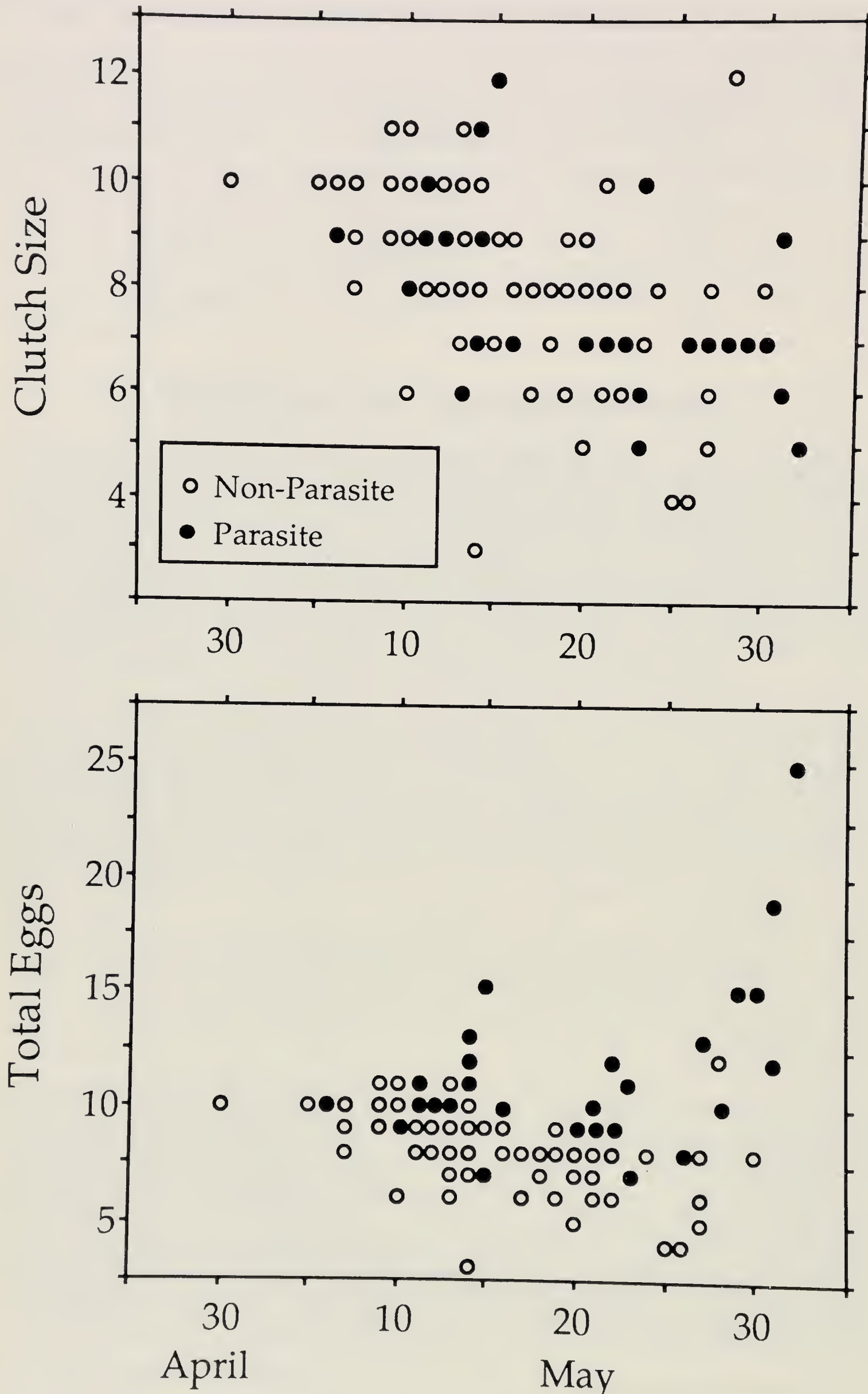


FIGURE 1 - A comparison of clutch sizes and total fecundities of parasites and non-parasites, as a function of laying date, at the Chilco West wetland site in 1989. TOP: Clutch size in parasites' own nests compared to clutch sizes of nonparasites. BOTTOM: 'Total fecundity' of parasites (i.e. own clutch plus parasitic eggs) compared with clutch size of nonparasites.

TABLE 2 - The success of parental and parasitic eggs in producing fledged offspring. ‘Parasites’ includes only territorial parasites, and does not include floaters or three females that parasitized after their own nests were destroyed. ‘Parental’ eggs includes all eggs that females lay in their own nests, including eggs destroyed by predation. In a few cases, parasite eggs hatched but their subsequent fate could not be determined. These eggs were assigned a fledging success equal to the proportion of hatched parasite eggs on the same lake that produced a fledged young.

	Total eggs	Fledged young	Proportion fledged	Success parasitic/ parental
Parental eggs				
1. All females	1133	342	.30	27%
2. Parasites only	237	80	.34	24%
Parasitic eggs	157	12.6	.08	

CONSTRAINTS OF PARENTAL CARE

Parasitism may be a strategy which allows females to circumvent some of the constraints of parental care, so I examined whether post-laying parental care constrains the number of chicks a pair can raise. American Coots are indeterminate layers and many females are capable of laying far more eggs in a continuous sequence than the number that they actually lay in their own nest. The evidence presented above indicates that this is true for parasites, but other observations show that this holds for many non-parasites as well. Most females whose nests were preyed upon before clutch completion renested immediately without skipping a day and laid a full-sized replacement clutch. Several such cases resulted in females laying 16 to 23 eggs in a continuous laying sequence of one egg per day.

Several observations indicate that reproductive success achieved through parenting is limited by post-hatch parental care. Brood reduction was pronounced in all three years of the study and most pairs lost several young, as is illustrated in Figure 2 for 1989. Some pairs lost nearly 90% of their brood, and losses of 30 to 50% were common. Hatching asynchrony was pronounced and, depending on the brood, hatch was spread over a three to seven day period. The pattern of mortality within broods was related to the hatch sequence. In focal broods followed in 1989, 58% of the first five chicks hatched (N = 104 chicks) survived to independence while only 25% of chicks that hatched sixth or later in the hatch sequence survived (N = 67). Intensive observations at focal nests in 1987 and 88 showed that most of this mortality was due to starvation. Most chick deaths occurred in the first two weeks after hatch when the chicks are dependent on the adults for food. Moreover, the bodies of most chicks that died were found intact on the territory, ruling out predation. In some cases where feeding watches were done for several hours, small chicks that were ignored and not fed all day by parents were found dead the following morning. Finally, frequent parental aggression toward chicks over food allocation (unpublished data) indicate that food is limited. These findings are similar to Horsfall’s (1984) observations for European Coots *Fulica atra*, but I never observed the direct infanticide that he observed.

Together, these observations indicate that female coots are capable of laying more eggs than they actually do in their own nests, and that the number of offspring that a pair can raise in their own nest is limited by the amount of food that they can supply.

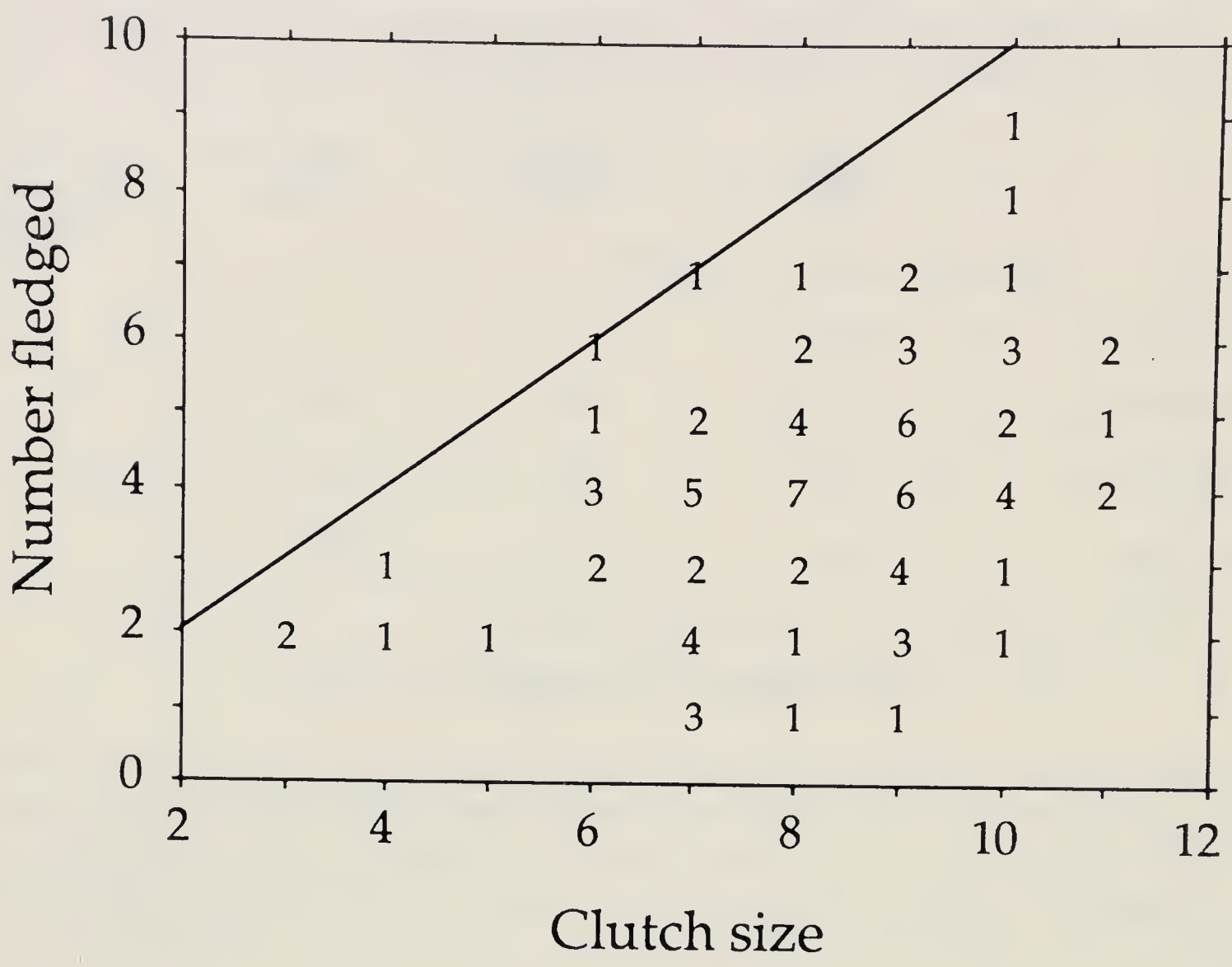


FIGURE 2 - The intensity of chick mortality in 1989, as shown by the fledging success of pairs with different clutch sizes. Numbers represent the number of pairs that had each clutch size - number fledged combination. The diagonal line indicates the number of young that would have fledged for each clutch size had there been no mortality. Observations indicate that this pattern of mortality represents brood reduction through starvation.

DISCUSSION

Why do some coots engage in brood parasitism? Some parasitism was by floater females without nests or territories of their own. It is difficult to determine why these females parasitized because their identities were not known. Other studies have suggested that non-territorial parasites are either young, unmated females (Yom-Tov 1980) or females that are unable to obtain a nest site or territory due to saturation (Lank et al. 1989). For coots in central British Columbia, territory limitation is probably the most important factor because almost all suitable breeding sites were occupied. Fights between neighbours over territory boundaries were intense and frequent throughout the entire breeding season, and many pairs attempted to breed on marginal territories where the probability of success was low (unpublished data).

A small fraction of the parasitism involved females whose nests were destroyed with partially completed clutches. In these cases, parasitism is probably a salvage strat-

egy which allows females to obtain some fitness from eggs that would otherwise be wasted because a replacement nest is not yet ready. Parasitism in response to nest destruction has been reported in other species (Yom-Tov 1980), and Emlen & Wrege (1986) were able to experimentally induce this behavior by blocking nest tunnels of White-fronted Bee-eaters *Merops bullockoides* that were laying eggs.

Most of the parasitism was attributed to females that had nests of their own, as is the case in most species where it has been possible to identify parasitic females (Clawson et al. 1979, Heusmann et al. 1980, Brown 1984, Gibbons 1986, Møller 1987). To understand how territorial female coots benefit from being parasitic, it is necessary to consider the tradeoffs involved. Parasites did not lay smaller clutches in their own nests than nonparasites, as would be expected if the primary benefit were to reduce the cost of raising chicks (Davies 1988). Furthermore, eggs laid parasitically were far less successful than the eggs that parasites laid in their own nest, demonstrating that parasitism does not benefit females by improving the quality of parental care their offspring receive (Brown & Brown 1988). If the main advantage to parasitism were to spread the risk of predation (Rubenstein 1982, Bulmer 1984), parasites should have laid the same total number of eggs as non-parasites, but simply rearranged this total among more nests. This was not observed. Parasites laid more total eggs than non-parasites, indicating that the most important benefit of parasitism is increased fecundity.

Increased fecundity is only a partial explanation for parasitism because it doesn't explain why parasites don't simply lay the extra eggs in their own nests. A complete explanation hinges on an understanding of how parental care constrains the number of young a pair can raise. Most pairs of coots are unable to raise all of the eggs they lay in their own nests because food for young is limiting, so it would make little sense for females to lay extra eggs in their own nests. Parasitism therefore allows territorial, nesting females to circumvent the constraints of parental care and increase their total production of offspring. In general, parasitism will always be favoured as an alternative reproductive tactic whenever birds can lay more eggs than they can rear, as long as the benefits that accrue from laying these 'parasitic' eggs exceed the fitness costs of producing them and getting them into the nests of other pairs.

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CONSTRAINT AND OPPORTUNITY IN THE EVOLUTION OF BROOD PARASITISM IN WATERFOWL

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ABSTRACT. An analysis of the phylogenetic distribution of intraspecific brood parasitism in the Anatidae revealed that parasitic behaviour is a primitive trait. Parasitism occurs throughout the family and the behaviour is not limited to any particular tribe or genus. Variation in the frequency of parasitism among species and among genera is correlated with several ecological factors; most notably, nest-site availability and host availability. I determined the influence of these factors in maintaining brood parasitism in two species of cavity-nesting ducks, the Barrow's Goldeneye *Bucephala islandica* and the Common Goldeneye *B. clangula*. The frequency of parasitism was inversely related to the availability of nest sites, whereas there was no correlation with host availability. Experimental manipulation of nest site densities confirmed the effect of nest limitation. Some females, however, laid parasitically even when suitable nest sites were abundant. These females laid 1-4 extra eggs in neighbouring nests and thereby increased their total reproductive output. I argue that parasitism in goldeneyes, and perhaps other waterfowl, is an opportunistic tactic pursued by females when they are either constrained from establishing their own nest or when there is an opportunity to lay additional parasitic eggs on the side.

Keywords: Barrow's Goldeneye, Common Goldeneye, *Bucephala islandica*, *Bucephala clangula*, brood parasitism, waterfowl, Anseriformes, Anatidae, breeding, phylogeny.

INTRODUCTION

Intraspecific brood parasitism is disproportionately common among precocial birds, particularly among waterfowl. Of the approximately 200 species of birds known to parasitize conspecifics, 71 species belong to a single family, the Anatidae (Eadie et al. 1988, Rohwer & Freeman 1989, Yom-Tov 1980). However, thirty years after Weller's (1959) inaugural study, there is still little consensus on the factors that promote brood parasitism in waterfowl. Numerous hypotheses have been proposed to explain parasitic behaviour (Andersson 1984, Eadie et al. 1988, Yom-Tov 1980), yet few of these alternatives have been tested.

Here, I examine some of the factors that influence intraspecific brood parasitism in the Anatidae. I first map the phylogenetic distribution of intraspecific brood parasitism among North American waterfowl to examine for phylogenetic constraints on parasitic behaviour. I then investigate the role of several ecological factors that might promote parasitic egg-laying. Finally, I ask whether these same factors influence the frequency of brood parasitism within, as well as among, species. I present the results of a four year study on facultative brood parasitism in two species of cavity-nesting ducks, the Barrow's Goldeneye *Bucephala islandica* and the Common Goldeneye *B. clangula*.

METHODS

Livezey (1986) derived a phylogeny of the recent Anseriform genera through a cladistic analysis of 120 morphological characters. I used this phylogeny to examine the distribution of brood parasitism among the 41 species of anatids native to North America. My analysis was restricted to these species because they have been studied most thoroughly, and data on parasitic behaviour and life histories are readily available (Bellrose 1976, Palmer 1976, Johnsgard 1978, Eadie et al. 1988, Rohwer 1988, Rohwer & Freeman 1989). I categorized the frequency of intraspecific brood parasitism as: (i) not reported; (ii) infrequent (reported by only one or two sources for restricted geographical areas); (iii) occasional (reported by several sources, although at low levels); and (iv) frequent (reported by most or all sources, noting high levels of parasitism in some populations) (after Eadie 1988).

TABLE 1 - Comparison of life history traits of North American anatids that exhibit occasional or frequent brood parasitism with those that exhibit parasitism rarely or not at all. Means \pm 1 SE with sample sizes in parentheses. Values in the first row for each variable are calculated for species, while values in the second row are for genera. Comparisons are by Mann-Whitney U-Tests.

Trait	Frequency of Brood Parasitism		
	Occasional or frequent		Rare or not reported
Female weight (g)	1098 \pm 194 (19)	NS	1637 \pm 465 (22)
	713 \pm 68 (7)	+	2009 \pm 780 (9)
Egg weight (g)	70.1 \pm 7.5 (19)	NS	86.4 \pm 17.4 (22)
	58.6 \pm 4.6 (7)	NS	101.6 \pm 29.1 (9)
Clutch size	8.8 \pm 0.5 (19)	*	7.0 \pm 0.5 (22)
	9.6 \pm 0.5 (7)	**	6.3 \pm 0.6 (9)
Maximum clutch size	14.8 \pm 0.7 (18)	**	11.4 \pm 0.8 (21)
	14.7 \pm 1.3 (7)	*	10.4 \pm 0.7 (9)
Egg-laying period (days)	54.1 \pm 6.0 (19)	*	35.7 \pm 5.3 (20)
	63.7 \pm 10.3 (7)	**	25.0 \pm 6.7 (9)
Incubation period (days)	27.4 \pm 0.6 (19)	*	25.4 \pm 0.7 (21)
	28.3 \pm 1.1 (7)	+	25.1 \pm 1.3 (9)
Maximum lifespan (years)	14.3 \pm 0.6 (19)	*	17.1 \pm 1.0 (16)
	13.1 \pm 0.6 (7)	NS	11.2 \pm 2.4 (9)
Age at maturity (years)	1.6 \pm 0.1 (19)	NS	2.0 \pm 0.2 (22)
	1.5 \pm 0.2 (7)	*	2.3 \pm 0.3 (9)

NS Not significant, + P < 0.10, * P < 0.05, ** P < 0.01

To investigate the factors that might promote brood parasitism, I extracted information on ecology and life history for each species from the above sources (Table 1). I then

compared these traits for species that exhibited frequent or occasional parasitism (hereafter referred to as parasitic species, N = 19) with species for which parasitism was rare or not reported (hereafter referred to as non-parasitic species, N = 22). To ensure that this analysis was not biased by a lack of taxonomic independence among species, I repeated these analyses using genera as the sample unit. Genera were categorized as parasitic or non-parasitic according to the frequency of parasitism in the majority of species in each genus.

Finally, I conducted a field study of brood parasitism in the Barrow's Goldeneye and the Common Goldeneye. A full description of the species, study area and methodology is presented elsewhere (Eadie 1989,1990). Briefly, I followed all nesting attempts in a population of goldeneyes breeding in central British Columbia, Canada. I monitored the frequency of parasitism, the identity of parasites, and the reproductive success of parasitic and non-parasitic females using nest cameras, nest traps, and detailed behavioural observations. I also manipulated the availability of nest sites to determine the influence of nest limitation on the frequency of parasitism (see below).

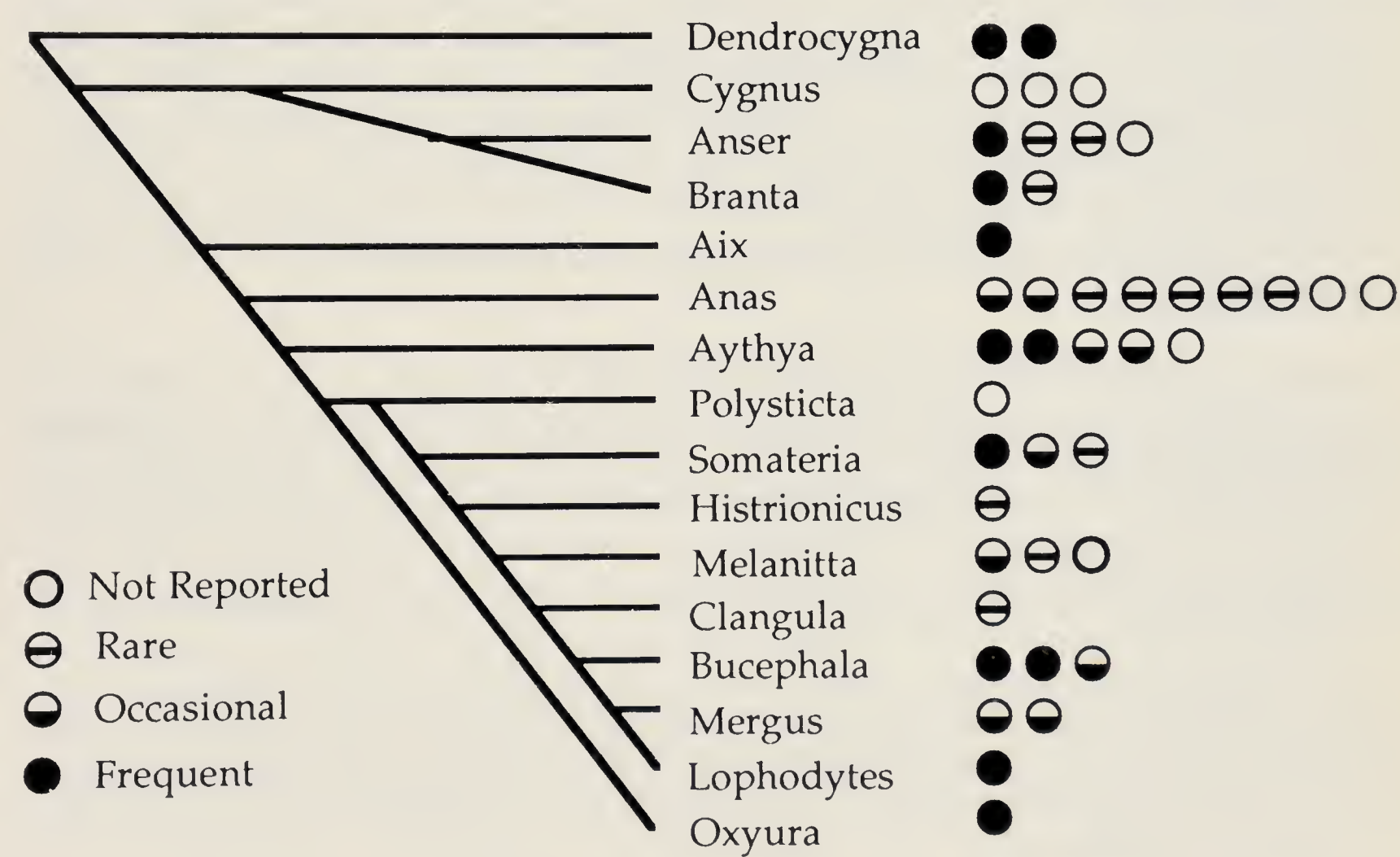


FIGURE 1 - The phylogenetic distribution of facultative brood parasitism in the North American Anatidae. Each circle represents a single species.

RESULTS

The phylogenetic distribution of brood parasitism in waterfowl

The distribution of intraspecific brood parasitism among North American waterfowl indicates that parasitic behaviour is a primitive trait (Figure 1). Parasitism occurs throughout the family, including species in older genera such as *Dendrocygna*, as well as species that have diverged more recently e.g. *Lophodytes*, *Oxyura*. Intraspecific brood parasitism has also been documented in all three outgroups of the

Anseriformes (Galliformes, Charadriiformes, and Ciconiformes; Livezey 1986). Thus, parasitism appears to be ancestral to the Anseriformes, and it is likely that all species in the order are capable of laying eggs parasitically.

Nonetheless, parasitism is not equally common in all species. For example, intraspecific brood parasitism has never been reported in any of the North American swans *Cygnus*, yet it is extremely common in the perching ducks *Dendrocygna*, some of the diving ducks *Aythya*, and some of the sea ducks *Bucephala*, *Mergus*. There is considerable variation even within members of the same genus e.g. *Anser*, *Anas*, *Aythya*, *Somateria*. Clearly, parasitic behaviour within the Anatidae is not phylogenetically constrained, and the observed variation among species must depend on other factors. A comparative analysis to search for these factors seems justified.

Correlates of brood parasitism in the Anatidae

I found differences between parasitic and non-parasitic anatids in several life-history traits. In general, parasitic species are characterized by larger clutch sizes, longer egg-laying periods (days between the initiation of the first and last nest), and longer incubation periods relative to non-parasitic species (Table 1). Parasitic species also tend to be smaller in size and exhibit an earlier age of maturity although these differences are marginal and depend on the taxonomic level of analysis. There is no difference in egg weight between parasitic and non-parasitic species, and a tendency for parasitic species to have shorter life spans is reversed when analysed at the genus level. Otherwise, all patterns found at the species level are similar to those found at the genus level.

Parasitic egg-laying is strongly related to the type of nest site. All seven species of cavity-nesting ducks are parasitic, four of six (67%) emergent nesters are parasitic, while only 8 of 20 (29%) upland nesters are parasitic ($G_w = 14.3$, $P < .001$). More-over, brood parasitism is more common in upland nesters that breed in close proximity on islands or in colonies (eight of 17 species are parasitic) compared with those that establish isolated nests on the mainland (none of 11 species are parasitic; $G_w = 8.30$, $P < .01$).

Finally, parasitism among North American anatids is related to the degree of female philopatry. Ten of 12 species with high levels of philopatry are frequent brood parasites compared with seven of the 17 species with low or moderate levels of philopatry ($G_w = 5.20$, $P < .03$).

Brood parasitism in Goldeneyes

The above analyses consider broad patterns among species. I next ask whether similar ecological factors influence the frequency of parasitism within species. Parasitic egg-laying was common in goldeneyes over the four years of my study with an average of 35% of all nests being parasitized and 17% of all eggs being laid parasitically.

Nest site availability had the single greatest influence on the rate of parasitism within goldeneyes. The frequency of parasitism was highly correlated with the proportion of nest sites used ($r_s = .80$, $P < .001$; Figure 2). Strikingly similar results emerged when I experimentally manipulated the number of nest boxes on four study lakes (Figure 3). The frequency of parasitism varied directly with the availability of nest boxes and all changes were in the predicted direction; that is, (1) there was no change in the pro-

portion of parasitized nests on the control lake, (2) the proportion of parasitized nests doubled on the nest reduction lake, and (3) the proportion of parasitized nests decreased sharply and then increased on the two nest addition lakes, with the changes matching closely the duration of the pulsed additions (Figure 3). Unfortunately, it was not possible to replicate these treatments and so I cannot assess the statistical validity of these results.

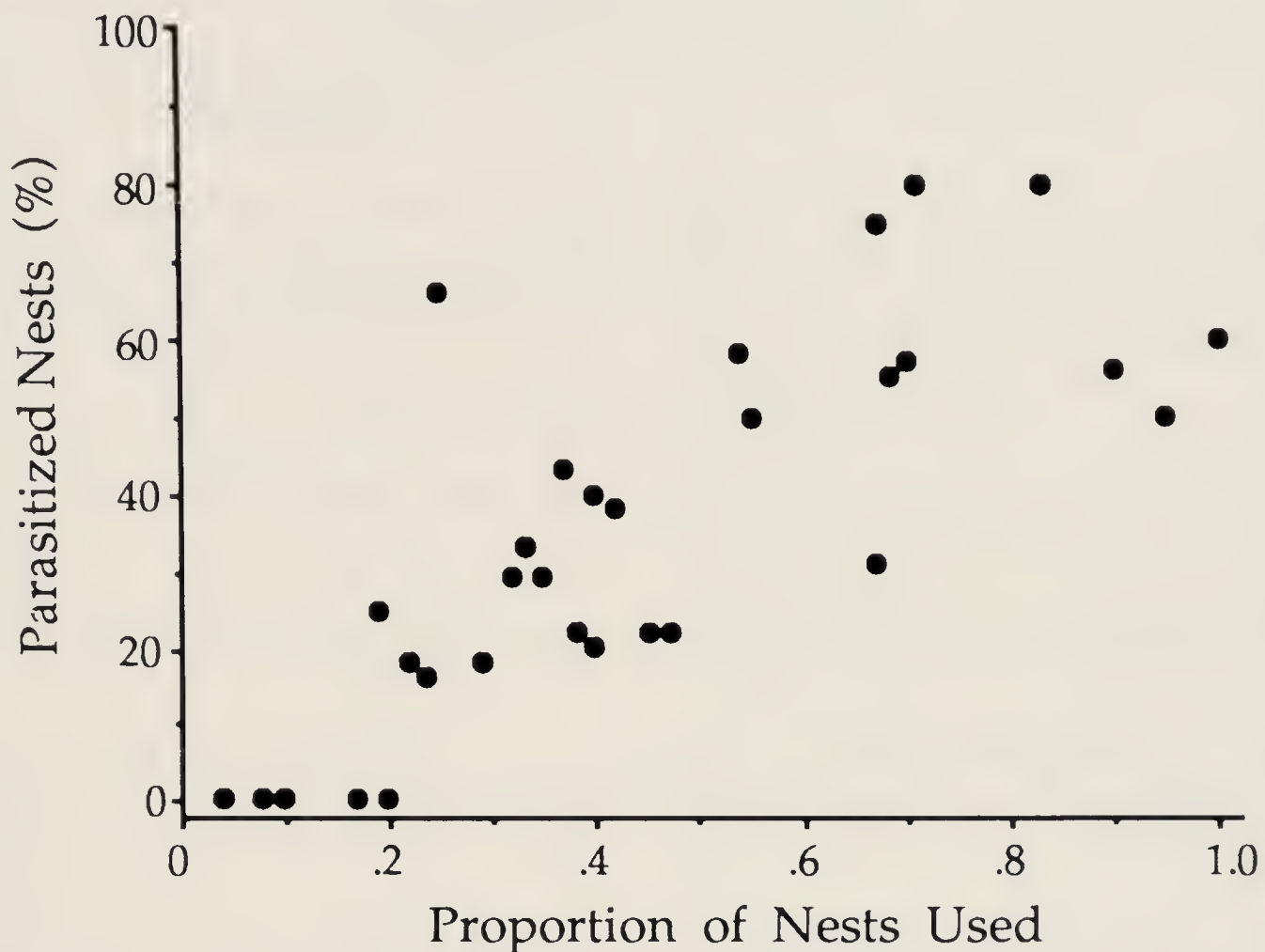


FIGURE 2 - The relationship between the frequency of brood parasitism in goldeneyes and the degree of nest site limitation. Each point represents a separate lake in a different year. The number of potential nest sites per lake ranged from 6 to 44.

An alternative explanation for the relationship between parasitism and nest limitation is that parasitic egg-laying is simply facilitated by an increased availability of hosts at high population densities (Rohwer & Freeman 1989). I used partial correlation analyses to separate these effects. The frequency of parasitism was not correlated with the number of host nests when either the number of nest boxes ($r_p = .19$, $N = 31$, $P > .10$) or the proportion of nests used ($r_p = -.23$, $P > .10$) was held constant. In contrast, when the number of hosts was controlled statistically, the frequency of parasitism remained significantly correlated with both the number of nest boxes ($r_p = -.49$, $P < .01$) and the proportion of nests used ($r_p = .77$, $P < .001$). Parasitic behaviour in goldeneyes therefore appears to be most strongly influenced by the availability of nest sites.

Nest limitation cannot, however, be the sole explanation for parasitism in goldeneyes since some parasitic egg-laying occurred even when suitable nest-sites were available (Figure 2). Furthermore, 10 of 33 parasitic females established their own nest while also laying parasitic eggs. In all of these cases, females parasitized a neighbour's nest located within 500 m on the same lake or pond. These females may have gained through increased egg production. Although parasitic eggs suffered lower hatch success (due to deposition of parasitic eggs after the start of incubation), parasites laid more eggs in total than non-parasitic females (Table 2). Estimated annual

reproductive success and lifetime reproductive success of parasitic females were therefore slightly greater than for parental females (Table 2).

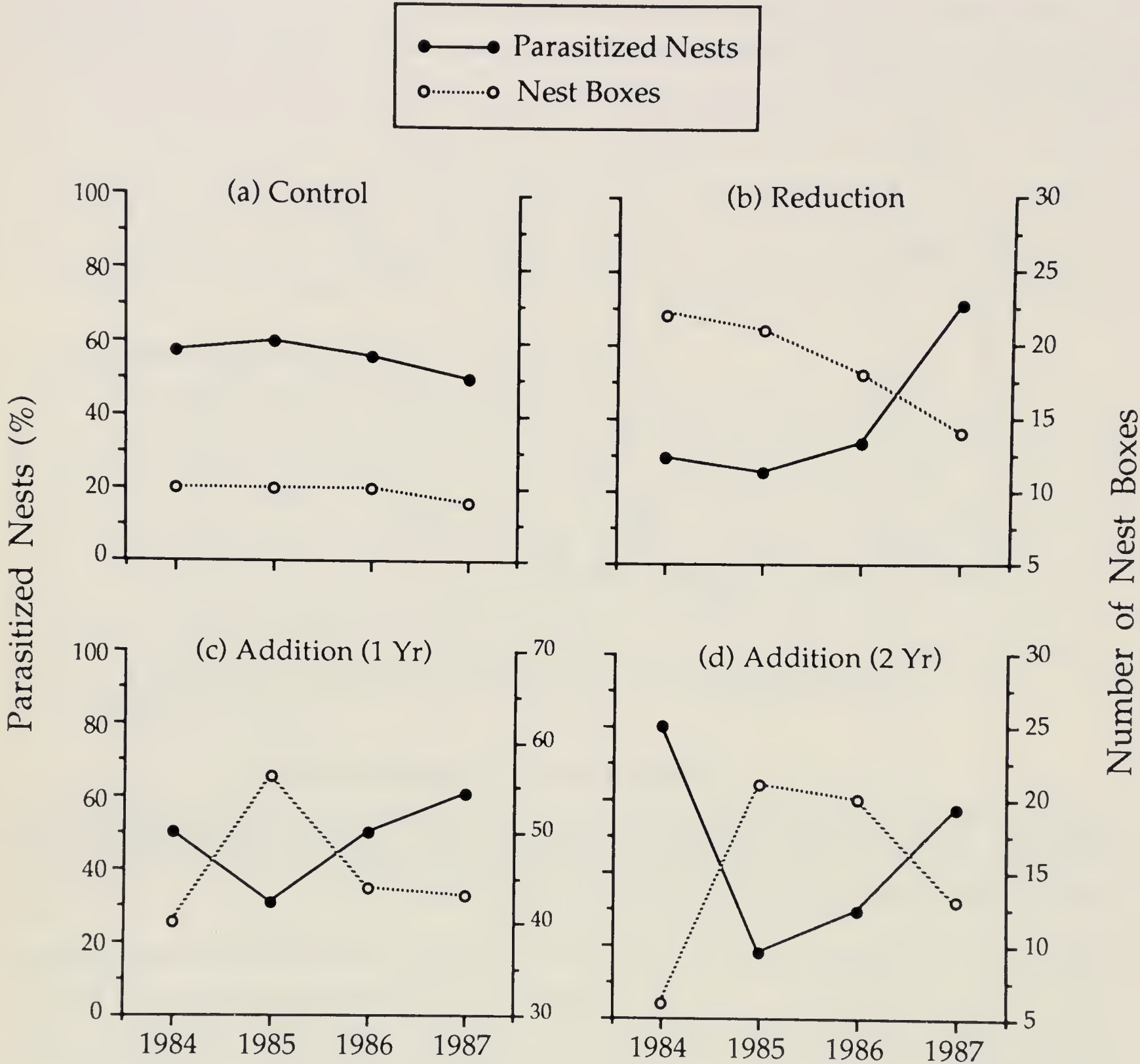


FIGURE 3 - The effect of experimental manipulations of nest site densities (open circles) on the frequency of brood parasitism (closed circles). Each graph represents a separate lake followed over four years. The number of nest sites used on each lake ranged from 5 to 39.

DISCUSSION

This study presents the first phylogenetic analysis of the distribution of brood parasitism within the Anatidae. The results of this analysis strongly suggest that parasitic behaviour is a primitive trait in waterfowl, and that all species probably have the ability to lay parasitic eggs. Thus, the fact that parasitism is not equally common in all species indicates that the expression of parasitic behaviour is constrained by ecological rather than phylogenetic factors. Indeed, I found differences between parasitic and non-parasitic anatids in several ecological and life history traits. Many of these traits were proposed by Andersson (1984) to account for the high frequency of brood parasitism in waterfowl relative to other birds. For example, Andersson (1984) proposed

that large clutch sizes and longer egg-laying periods could promote high frequencies of parasitism because parasites would have a longer period over which to locate host nests. I found that parasitic anatids did indeed have larger clutches and longer egg-laying periods. Similarly, Andersson (1984) thought that parasitism might be facilitated in the Anatidae by kin selection, since females are the philopatric sex in most waterfowl. As predicted, parasitism is more common in anatids exhibiting high levels of philopatry. However, even if kin selection were operating, it would only address the issue of why parasitism is tolerated by hosts. It would not explain why females lay parasitically in the first place.

TABLE 2 - Reproductive success of parasitic and parental goldeneye females. Means \pm 1 SE with sample sizes in parentheses. Values in the same row with different superscript letters are significantly different ($P < .05$; Mann-Whitney U-tests).

	Parasitic Females	Parental Females Alone	Parasitized
Clutch Size ¹			
a) Observed	9.0 \pm 0.5 ^a (12)	8.1 + 0.2 ^{a,b} (50)	7.8 \pm 0.2 ^b (66)
b) POFs	10.0 \pm 0.3 ^a (7)	8.0 \pm 0.0 ^b (2)	8.3 + 0.4 ^b (7)
Nest success (%)	0.76 \pm .04 ^a (102)	0.72 \pm .05 ^a (71)	0.76 \pm .04 ^a (102)
Hatch success (%)	0.74 \pm .04 ^a (59)	0.92 \pm .03 ^b (40)	0.89 \pm .02 ^b (59)
Fledge success (%)	0.46 \pm .05 ^a (48)	0.42 \pm .06 ^a (27)	0.46 \pm .05 ^a (48)
Breeding Lifespan (years)	2.11 \pm 0.19 ^a (19)	1.84 \pm 0.11 ^a (61)	
Annual reproductive Success ²	2.33 2.59	2.31 2.36	
Lifetime reproductive Success ²	4.91 5.47	4.26 4.35	

¹ Clutch size was estimated by following the laying activities of individual females (Observed) and through counts of post-ovulatory follicles (POFs).

² Annual success (number of fledglings) is estimated as the product of clutch size, nest success, hatch success, and fledge success. Lifetime success is the product of breeding lifespan and annual success. Estimates are based on 38% of parental nests being parasitized and are calculated using both observed clutch sizes (top value) and POF counts (lower value).

One of the clearest patterns to emerge from the comparative analysis was the relationship between nest type and the frequency of parasitism. Similar patterns have been noted by other authors (Eadie et al. 1988, Rohwer & Freeman 1989), although there is disagreement over the underlying mechanism. Eadie et al. (1988) suggested

that frequent parasitism in cavity-nesting birds reflected the influence of nest-site limitation, whereas Rohwer & Freeman (1989) argued for an influence of host availability and ease of locating host nests. Results of the comparative analysis presented here support the host availability hypothesis. Parasitism among upland nesting waterfowl is more common in colonial and island nesting species than in species establishing isolated nests on the mainland (see also Rohwer & Freeman 1989). Although it is possible that suitable nest sites or nest territories are limited in colonies or in dense nesting aggregations, these data are more consistent with the notion that high densities of potential hosts in colonies and on islands facilitate the opportunity to lay parasitic eggs (Rohwer & Freeman 1989).

The results of the comparative analyses should be viewed with caution. Analyses using species as the taxonomic unit can be biased by phylogenetic constraints and by a lack of statistical independence among species. However, parasitic behaviour does not appear to be phylogenetically constrained in the Anatidae, and analyses using genera instead of species produced virtually the same patterns. Nonetheless, these analyses do not allow one to separate causation from correlation. For example, the larger clutch sizes and longer incubation periods of parasitic species (Table 2) may simply be a consequence and not a cause of frequent brood parasitism. Detailed analyses within species are required to separate these effects.

Analyses of parasitic behaviour within goldeneyes corroborated the strong relationship between nest sites and the frequency of parasitism. However, in this case, host availability could not account for the relationship. Both experimental and observational data indicate that parasitism in goldeneyes is more directly influenced by nest site limitation (Figures 2 and 3; Table 1). Patterns identified by comparative analyses among species, therefore, do not necessarily implicate the same causal mechanism for similar patterns identified within species. Nonetheless, it seems clear that both host availability and nest limitation play some role in facilitating brood parasitism in waterfowl.

Analyses of parasitic behaviour within goldeneyes also indicate that more than one factor can promote parasitic egg-laying. Despite the strong relationship between parasitism and nest site availability, moderate frequencies of parasitism occurred even when unoccupied nest sites were available (Figure 2). Many of these nest sites had been used successfully in previous years indicating that they were suitable for goldeneyes. Some females also laid eggs as brood parasites before or during the period that they established a nest of their own. These females appeared to lay parasitic eggs as an opportunistic or side-payment tactic, whereby they produced more eggs in total and thus enhanced their net reproductive success. This raises an important question — since precocial birds can generally raise more young than they normally produce (Rohwer 1984), why wouldn't a female simply lay all of her eggs in her own nest? There may be at least five ways that a precocial parasite might gain through parasitic egg-laying:

- (1) Females that breed solely by parasitism may be able to channel the energy saved by avoiding incubation and brood rearing into increased egg production. Even females that establish their own nest in addition to laying parasitically might be able to produce more eggs by spreading out the demands of egg production (Heusmann et al. 1980).

- (2) Parasitism might be advantageous if some factor other than energy or nutrients limits the number of eggs that a female can lay in her own nest. For example, clutch size in ducks may be limited by egg viability — eggs that are not incubated within a certain number of days may not hatch (Arnold et al. 1987). By laying some eggs parasitically prior to establishing their own nests, females could avoid this constraint.
- (3) Parasitism might be advantageous if females were able to secure better care for their offspring than they could provide themselves. This might benefit young females, in particular, if they were able to parasitize older, more experienced hens.
- (4) Parasitic behaviour might enhance the survival and, therefore, the lifetime fitness of females by eliminating the time and energy costs associated with incubation and brood-rearing.
- (5) Finally, by spreading eggs among several nests, a parasite could reduce the risk of total nest failure and thereby increase the probability that at least some young survive (Payne 1977, Rubenstein 1982, but see Bulmer 1984, Eadie 1989).

In summary, the results of my study and other recent studies (Andersson 1984, Lank et al. 1989, Rohwer & Freeman 1989) indicate that two general factors promote facultative brood parasitism in waterfowl. First, parasitism appears to be favoured in species faced with frequent constraints on parental nesting. Nest site availability is the limiting constraint for goldeneyes, but other factors such as frequent nest loss, limited breeding experience, or reduced body condition may constrain breeding opportunities in other species (reviews in Eadie et al. 1988, Lank et al. 1989). Parasitism of conspecifics would allow females to salvage some reproductive success during periods when they are unable to (or when it does not pay to) breed otherwise.

Second, parasitism appears to be favoured in species for which potential hosts are readily available and easily located. Since the success of the parasitic tactic ultimately depends on the availability of suitable hosts, it is not surprising that parasitism is more common in species for which there is ample opportunity to parasitize other individuals. I believe that these dual themes, constraint and opportunity, can explain much of the variation in the frequency of parasitism among the Anatidae. Moreover, both factors might explain some of the variation found within species. For example, young or inexperienced females might pursue parasitism in response to constraints or restraints on normal breeding, whereas older females might pursue parasitism as a side-payment strategy in order to increase their net fecundity. Further studies of the ontogenetic development of parasitic behaviour would therefore prove revealing. It will also be interesting to determine if similar patterns are found in other species of birds (Haland 1986), insects (Tallamy 1985, 1986) and fishes (Sato 1986) in which frequent parasitism of conspecifics has been observed.

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EVOLUTION OF INTRASPECIFIC VARIABILITY IN BIRDS' EGGS: IS INTRASPECIFIC NEST PARASITISM THE SELECTIVE AGENT?

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ABSTRACT. The amount of variability in size, shape, colour and pattern of eggs within and between clutches varies between bird species. The main hypotheses accounting for this variability are (1) the nest predation hypothesis and (2) the intraspecific nest parasitism hypothesis. The nest predation hypothesis states that egg variability is an evolutionary response to predation. If nest predators are searching visually, it would pay individuals of prey species to produce cryptic eggs. Eggs which differ from the norm both within and between clutches would be more likely to be detected by predators. The intraspecific nest parasitism hypothesis states that egg variability is an evolutionary response to intraspecific nest parasitism. Individuals who produced distinctly patterned eggs with little intra-clutch variation are more likely to recognize the presence of a 'foreign' egg. We tested these ideas (1) by determining whether the risk of intraspecific nest parasitism in the Moorhen *Gallinula chloropus* is related to the deviation in appearance of a particular clutch from the population mean, and (2) by comparing intra- and inter-clutch variation in egg appearance in closely related pairs of less and more socially breeding bird species. The risk of intraspecific nest parasitism has been shown to be larger in social species. Therefore we would expect less intra-clutch and more inter-clutch egg variability in socially than in solitarily breeding bird species. However, the risk of nest predation is supposed to be smaller in colonial species, and under these circumstances we would predict more intra- and inter-clutch variability in colonial species. We found that there was less intra-clutch variation in more social species and that those Moorhens with more foreign eggs in their clutches also had more pigment on their eggs.

Keywords: Intraspecific nest parasitism, interspecific nest parasitism, Moorhen, *Gallinula chloropus*, intra-clutch egg variability, inter-clutch egg variability, nest predation.

INTRODUCTION

The eggs of bird species vary in appearance, from uniformly coloured and shaped in some species to extremely polymorphic. For example, in weaverbirds some females lay blue, others red and still others white eggs. This phenomenon is clearly demonstrated in handbooks where the eggs of some species need several plates to be thoroughly illustrated, whereas a single plate is sufficient for the eggs of others. There are two main hypotheses which could account for this intra- and interspecific variability.

First, nest predation could be an important selective agent modifying the appearance of birds' eggs. Here, individuals of bird species which have eggs deviating from the population mean are assumed to suffer from increased nest predation rates. This leads to stabilizing selection on egg appearance, and, in accordance with this prediction, species suffering from intense nest predation generally have cryptic eggs (e.g. Tinbergen 1967, Lack 1968, Montevicchi 1977). Similarly, one could also argue that intra-clutch variation in the appearance of eggs should affect the risk of nest predation by visually searching nest predators, and, under these circumstances, strong stabilizing selection should lead to little intra-clutch variation in species suffering from intense nest predation at the nesting stage.

The second hypothesis relates to brood parasitism. The reproductive success of hosts is often reduced by the detrimental effects of intra- and inter-specific nest parasites. The resulting evolutionary arms race between nest parasites and their hosts puts a high premium on the ability of hosts to separate their own eggs from those of strangers, thereby allowing ejection of parasite eggs. Nest parasitism should therefore lead to stabilizing selection on intra-clutch variation in the appearance of eggs, since eggs of a homogeneous appearance often would allow recognition of deviating parasite eggs. Similarly, nest parasitism should lead to disruptive selection on inter-clutch variation in the appearance of eggs. Clutches deviating from the population mean would allow host discrimination against eggs of nest parasites. Under these circumstances, it would also be difficult for a nest parasite to specialize on a rare type of potential host eggs in a population, and individuals laying eggs deviating from the population mean should thus become parasitized less often than others. Disruptive selection would, on the other hand, have associated costs like increased predation by visually searching nest predators and decreased possibilities for individuals of becoming parasites themselves.

The frequency of nest predation generally is assumed to decrease with increasing sociality (Lack 1968, Ricklefs 1969), whereas the frequency of intraspecific nest parasitism increases with increasing sociality (Brown 1984, Møller 1987a, b, Rohwer & Freeman 1989). It is possible to generate a set of mutually exclusive predictions for egg variability in relation to social breeding. If the nest predation hypothesis accounts for egg variability, we would predict more intra-clutch and inter-clutch egg variability in social species, whereas the nest parasitism hypothesis predicts more intra-clutch variability in solitary species and more inter-clutch variability in social species.

We evaluated these two hypotheses (1) by comparing intra- and inter-clutch variation in egg appearance in closely related pairs of less and more socially breeding bird species, and (2) by determining whether the risk of intraspecific nest parasitism in the Moorhen *Gallinula chloropus* was related to the deviation in appearance of a particular clutch from the population mean.

METHODS

Interspecific test

We chose 15 closely related pairs of less and more socially breeding bird species, and for each we took colour photographs against a similar background of 10 randomly chosen clutches from the museum collections at the British Museum of Natural History, Tring, UK. Five students were then asked first to score intra-clutch variation in the appearance of eggs of all species and also to score inter-clutch variation. The students were not informed about the rationale behind the study or allowed to watch other students give scores, and they were not allowed to provide each other with information about the scores. Species pairs were placed in random order by A.P.M. and the more or the less social species of a pair was randomly placed first. All photographs of clutches of a single species were placed on a table and each clutch was given a single score based on egg size, egg shape, egg colour and the size, number and distribution of egg spots. It was assumed that all these visual cues could be used by birds discriminating between own and foreign eggs. Scores were on a five grade scale: (1) No variation. All eggs alike. (2) At least one egg slightly different, can barely

be distinguished. (3) At least one egg markedly different from the rest. (4) At least one egg dramatically different from the rest. (5) All eggs dramatically different. Inter-clutch variation was similarly scored on a five grade scale, by paying attention to all photographs of the 10 clutches of each species simultaneously: (1) No variation. All clutches alike. (2) At least one clutch slightly different, can barely be distinguished. (3) At least one clutch markedly different from the rest. (4) At least one clutch dramatically different from the rest. (5) All clutches dramatically different.

We tested for consistency in scores between students by calculating Kendall coefficients of concordance (Siegel 1956). Since pairs of closely related species only differed in social dispersion, differences in intra- and inter-clutch variation in the appearance of eggs due to the effects of the evolution of sociality could not be constrained by phylogeny (Felsenstein 1985). Differences in the mean scores of such species pairs could then be used as independent observations under the null hypothesis that differences did not deviate from 0. This was tested using a binomial test (Siegel 1956).

Intraspecific test

The data were collected over the breeding seasons 1983-1984 at a study site in Norfolk, UK (see Petrie 1984). Nests were found by observation and by searching emergent vegetation of the waterways. Differences between eggs laid by different individuals were quantified by measuring a number of parameters of each egg. Three colour transparencies of entire clutches were taken and the following measures taken from the enlarged image of each egg: (1) length, (2) width, (3) depth, (4) shape of narrow and of (5) broad end, (6) mean diameter of five largest spots on broad and (7) narrow end, (8) mean distance of 10 nearest spots to the centre of the broad and (9) narrow end, (10) weight. A spot was defined as any mark with a diameter greater than 0.5 mm after enlargement. These data were analysed using the SPSS discriminant function analysis. All ten variables were useful in determining whether or not an egg belonged to a clutch of eggs or whether it had a higher probability of belonging to another group, i.e. it was more similar to another clutch. All eggs which were indicated as outliers to a clutch were thought to be laid by parasites. The main evidence to support this is that when dumping was suspected in a nest, for example if an egg appeared outside the normal laying sequence, in some cases up to 12 days after incubation has started, the statistical treatment always indicated that these eggs were outliers. For more details of this method of identifying dumped eggs see Petrie and Hotchin (Ms).

The pigment present on the eggs was measured as the mean diameter of the five largest spots present on the 'broad' end. The 'broad' end was used as this contained the most pigment and showed the most variation between individuals. For each clutch a mean value was taken for all eggs excluding any that were indicated as outliers.

RESULTS

Interspecific comparative study

Students were highly consistent in their scores of intra-clutch variation in the appearance of eggs, and scores were significantly consistent in all 30 species (Table 1). Likewise, the students were also highly consistent in their scores of inter-clutch variation ($W=0.86$, $\chi^2=82.83$, d.f.=23, $P<0.001$). Clutches and species were therefore assigned a mean score based on the scores by all students.

TABLE 1 - Intra-clutch and inter-clutch variability in egg appearance for closely related pairs of more and less socially breeding bird species. Kendall's coefficient of concordance for scores by five persons measured the reliability of the within clutch scores.

Species	Egg score (mean (S.D.))		Coefficient of concordance within clutches
	Within clutches	Between clutches	
<i>Falco naumanni</i>	2.34 (0.53)	2.80 (0.45)	0.76***
<i>Falco tinnunculus</i>	2.58 (0.45)	3.60 (0.55)	0.67***
<i>Falco vespertinus</i>	2.14 (0.45)	3.10 (0.45)	0.70***
<i>Falco columbarius</i>	2.50 (0.55)	3.60 (0.55)	0.59**
<i>Falco eleonora</i>	1.98 (0.36)	3.40 (0.55)	0.73***
<i>Falco subbuteo</i>	2.42 (0.66)	3.60 (0.55)	0.42*
<i>Hirundo pyrrhonota</i>	2.11 (0.49)	3.80 (0.45)	0.78***
<i>Hirundo rustica</i>	2.32 (0.31)	3.60 (0.55)	0.74***
<i>Bombycilla cedrorum</i>	1.70 (0.39)	1.80 (0.45)	0.59**
<i>Bombycilla garrulus</i>	2.00 (0.33)	1.60 (0.55)	0.47*
<i>Turdus pilaris</i>	1.92 (0.60)	3.80 (0.45)	0.74***
<i>Turdus merula</i>	2.20 (0.64)	3.20 (0.45)	0.44*
<i>Sturnus roseus</i>	1.52 (0.34)	2.40 (0.55)	0.45*
<i>Sturnus vulgaris</i>	1.34 (0.30)	1.20 (0.45)	0.44*
<i>Pica nuttalli</i>	1.47 (0.28)	2.60 (0.55)	0.50*
<i>Pica pica</i>	1.86 (0.51)	2.80 (0.45)	0.68***
<i>Corvus monedula</i>	2.12 (0.66)	3.60 (0.55)	0.85***
<i>Corvus splendens</i>	2.53 (0.47)	3.20 (0.45)	0.71***
<i>Corvus frugilegus</i>	2.26 (0.65)	2.80 (0.45)	0.93***
<i>Corvus corone</i>	2.46 (0.78)	3.60 (0.55)	0.72***
<i>Passer hispaniolensis</i>	1.96 (0.64)	3.20 (0.45)	0.88***
<i>Passer domesticus</i>	2.48 (0.69)	2.60 (0.45)	0.74***
<i>Ploceus subaureus</i>	1.74 (0.55)	2.60 (0.55)	0.66***
<i>Ploceus castanops</i>	1.78 (0.49)	4.00 (0.71)	0.76***
<i>Fringilla montifringilla</i>	1.66 (0.37)	3.20 (0.84)	0.63***
<i>Fringilla coelebs</i>	1.92 (0.50)	3.60 (0.55)	0.41*
<i>Quiscalus mexicanus</i>	1.89 (0.44)	3.00 (0.71)	0.63***
<i>Quiscalus quiscula</i>	2.36 (0.56)	3.00 (0.71)	0.57**
<i>Xanthocephalus</i> <i>xanthocephalus</i>	1.92 (0.45)	2.00 (0.71)	0.58**
<i>Agelaius phoeniceus</i>	2.30 (0.46)	2.60 (0.55)	0.58**

* P < 0.05, ** P < 0.01, *** P < 0.001

Intra-clutch variation in the appearance of eggs was higher in the less than in the more social species in all 15 pairs of species (Table 1), significantly more often than expected by chance (binomial test, $P < 0.001$). Consistency in the scores of clutches of a single species by different students can be used as a measure of similarity in the appearance of clutches, distinctness of clutches leading to high consistency. Kendall coefficients of concordance were higher for more than for less socially breeding species in 13 out of 15 cases (Table 1), again a statistically significant difference (binomial test, $P < 0.029$).

Inter-clutch variation was not more pronounced in more as compared to less socially breeding bird species since mean scores for social species exceeded those for solitary species only in 8 out of 14 species pairs (Table 1; binomial test, N.S.).

Intraspecific test

There was a large amount of variability in the amount of pigment present on the eggs laid by different Moorhens. Hens also produce similarly patterned eggs in a clutch and it is possible to detect the presence of foreign eggs using a visual assessment mainly based on egg pigmentation (Gibbons 1986). The number of foreign eggs a nest receives also varies (range 0-4) and some hens are consistently parasitised more often and by more parasites than others. Petrie & Hotchin (MS) show that lighter, subordinate females are more likely to receive dumped eggs and be parasitised by a number of other hens.

There was a significant positive correlation between the average amount of pigment of the eggs in a clutch and the number of dumped eggs present ($r_s = 0.24$, $n = 64$, $P < 0.05$). Those clutches that had the most dumped eggs also had the most pigment on their eggs (Figure 1).

StatWorks™ Data spot size moorhen eggs Fri, Nov 9, 1990 2:31 pm

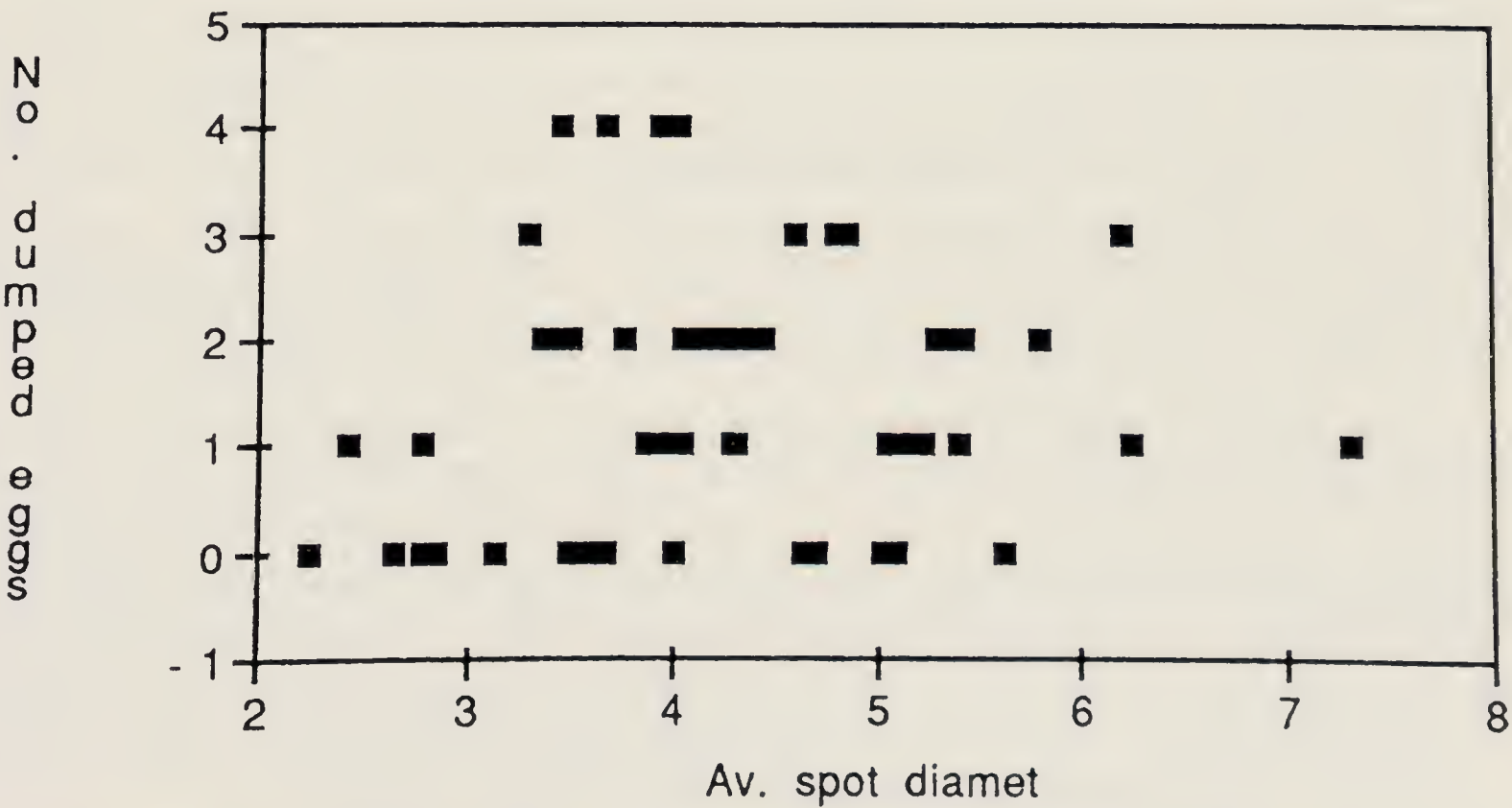


FIGURE 1 - Number of dumped Moorhen eggs in relation to the average spot diameter of the Moorhen hosts. $r_s = 0.24$, $N = 64$, $P < 0.05$.

DISCUSSION

Materials used for production of eggs are costly, and small, less colourful eggs should *ceteris paribus* be less costly than large colourful eggs (Murton & Westwood 1977). This is the common explanation for bird species often laying less colourful eggs late during the laying sequence (e.g. Lowther 1988). Costs of producing similarly sized and coloured eggs must, therefore, be balanced by benefits such as reduced nest predation or nest parasitism.

Both the size and the general appearance of eggs show consistency for particular females in subsequent clutches and years, and egg traits like size, colour and spot patterns generally show a large amount of heritable variation (e.g. Victoria 1972, Collias 1980, Laurila 1988, Thomas et al. 1989). Egg features thus could change dramatically provided the existence of a selection pressure like nest predation or nest parasitism.

The interspecific comparison clearly showed that less social species had larger intra-clutch variability in egg appearance than had more social species. Consistency in scores of intra-clutch variability were larger for social species suggesting that it was easier to assign a uniform score to clutches of such species. This is clearly in accordance with the nest parasitism hypothesis, but contrary to the prediction of the nest predation hypothesis. Since clutches already suffering from intraspecific nest parasitism are likely to be included in the data set, but more often so for social than for solitary species, the interspecific test is a conservative one. The prediction for inter-clutch variability in eggs was not supported by our data, suggesting either that this prediction is wrong or that the test was inappropriate. Freeman (1988) tested this prediction within the very homogeneous group of *Ploceus* weavers and found clear indications that inter-clutch variability is larger in highly social as compared to solitarily breeding species. Although his test may be biased because species cannot be treated as independent observations (Freeman 1988), the result suggests that the prediction may be supported if the ecological conditions are restricted.

The nest predation hypothesis has not found general support from field studies, since some experiments have suggested that predators cause stabilizing selection on egg appearance (Tinbergen 1967), whereas others do not (Montevecchi 1977). Field experiments have only been conducted on colonially breeding gulls, while use of the whole range of sociality might give a more clearcut result. Some of the experiments were also based on small sample sizes leading to a low power of statistical tests.

A third hypothesis suggests that egg appearance has changed because of interspecific nest parasitism (Swynnerton 1918, Davies & Brooke 1989). This hypothesis predicts that species with a history of interaction with cuckoos have distinctly marked eggs, and that they should have less intra-clutch and more inter-clutch variation than species not exploited (Davies & Brooke 1989). These predictions were clearly not supported when tested on British passerines interacting with Cuckoos *Cuculus canorus* (Davies & Brooke 1989), suggesting that selection pressures other than interspecific nest parasitism are responsible for egg variability.

The nest parasitism hypothesis assumes that eggs which differed from the population mean would allow for host discrimination against the eggs of parasites. The

intraspecific study of Moorhens showed that individuals which were susceptible to nest parasitism also had the most pigment on their eggs. That females susceptible to parasitism should produce distinctly marked eggs is not a prediction of the predation hypothesis.

Investment in the production of egg pigment is clearly not preventing parasitism completely, although we don't know how much more parasitism could have occurred. It may be important for an individual Moorhen to know whether or not parasitism has occurred. Birds may then have the option of ejecting the eggs of a parasite or they may decide to abandon the clutch entirely. Egg ejection is not thought to occur commonly in the Moorhen, since artificially introduced eggs are not ejected (M.P. unpubl. obs.), but, rarely, eggs have been found outside nests. Nest desertion does occur in the Moorhen, and all of the heavily parasitised nests found in this study with large clutch sizes (> 10 eggs) were deserted.

Moorhens that are susceptible to parasitism put more pigment on their eggs. They are using the costly option of producing pigment to make their eggs look different. Why don't females produce eggs which contain no pigment at all, as these eggs will look different from those of other females in the population? The answer to this probably lies in the fact that a parasite needs to mimic the egg patterns of the host to avoid detection. By adding pigment the host is effectively increasing the costs to the parasite. An unpigmented egg will be relatively less costly to mimic. Another possible explanation is that for a species with normally pigmented eggs, unpigmented eggs may be more visible to predators, if this was the case reducing pigment could carry other costs.

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SYMPOSIUM 16

FILIAL AND SEXUAL IMPRINTING

Conveners C. TEN CATE and A. B. DYER

SYMPOSIUM 16

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INTRODUCTORY REMARKS: FILIAL AND SEXUAL IMPRINTING – CAUSES AND CONSEQUENCES

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The phenomenon of young chicks becoming attached to flickering lights, or following humans in preference of conspecifics, has fascinated many ornithologists. It has long been known (Spalding 1873) that this behaviour may arise when these alternative stimuli, rather than a parent, are encountered soon after hatching. As the following response emerges very rapidly and, it was thought at the time, without reinforcement being involved, the development of the attachment seemed to involve a unique kind of learning process. Hence it was given a name of its own, which emphasized its instantaneous character and long-lasting influence: filial imprinting. Konrad Lorenz, who brought the subject to the attention of a wide audience with the publication (Lorenz 1935) and translation (Lorenz 1937) of his famous paper “Der Kumpan in der Umwelt des Vogels”, also suggested that the young bird’s early experience may have consequences for later sexual preferences. When birds that were raised by another species are adult, they may attempt to mate with birds of their foster species rather than with conspecifics, a phenomenon which has become known as ‘sexual imprinting’.

Lorenz also made strong claims concerning the unique features of imprinting: he saw the process as occurring in the absence of reinforcement, during a so-called ‘critical period’ and as being irreversible. His ideas stimulated much further research and became both a source of inspiration and a target for criticism. As a result much experimental work on imprinting came to focus on confirming or refuting various claims about the unique character of the process. This work flourished in the sixties and early seventies (for reviews of this earlier work, see Bateson 1966, Sluckin 1972). The dust settled on the controversies when increasing empirical evidence led to more sophisticated theories and when it became clear that the features of the imprinting process were less absolute than the earlier claims would have us believe.

Recent years show a revival of interest for the phenomenon of imprinting and the aim of this symposium is to present the current ‘state of the art’. It serves to show that the field is still very much alive and incorporates, as well as contributes to, developments in other areas. It demonstrates that, although the subject is a ‘classic’ subject for ornithological and ethological research, it certainly is not an ‘old fashioned’ one.

For a long time imprinting has served as a model for studying fundamental properties of behavioural development and, in particular, for examining the effects of external influences. In modern developmental studies the emphasis has shifted from simply demonstrating that early experience has an effect towards understanding just how such effects are brought about (e.g. ten Cate 1989). This change in attitude reflects the realization that setting up a dichotomy in behaviour between ‘innate’ and ‘learned’ parts does not help very much in understanding behavioural development. In his

contribution, Bateson describes how this modern theoretical stand has both strengthened and been strengthened by research on imprinting. He analyses the interplay between a 'predisposition' in Domestic Fowl *Gallus domesticus* chicks to respond to particular 'naturalistic' objects and the plasticity which the birds show in incorporating experience with other objects into their final filial preference. His paper serves as a good introduction to the symposium, as several of the issues he discusses return in later contributions.

Asking questions about the causal mechanism involved in filial imprinting ('how the job is done') may benefit from asking functional questions ('why the job is done') and vice versa. This approach is reflected in Dyer's contribution. She represents a school, founded by Gottlieb and co-workers, in which the research on filial imprinting is strongly guided by considering the natural context of the process. Dyer shows how this may give rise to experiments which examine the role of siblings or that of acoustic stimuli from the mother. The results of these studies make her challenge the implicit assumption in much laboratory work, which is that filial imprinting serves mainly for recognition of the mother. Instead she argues that visual imprinting may primarily serve to recognize brood mates, while bonding to the mother, at least initially, is guided by her vocalisations.

An area of research for which imprinting has always served as a model is that into the causation and regulation of sensitive phases in development. In the past these phases have frequently been seen as quite strictly delineated periods, reflecting age related changes in the individual. Kruijt's contribution to this symposium provides a clear example refuting this view. His work on sexual imprinting in Zebra Finches *Taeniopygia guttata* not only demonstrates, as have other studies, that birds may modify their sexual preferences in adulthood, but, in addition, he demonstrates that the potential to do so is strongly countered if the adult bird is given a short period of exposure to individuals of the rearing species. The latter finding is surprising and intriguing as it suggests that preferences acquired earlier require a specific experience to become consolidated. This result suggests that, at least in this case, a sensitive phase, usually viewed as a simple, age-dependent, phenomenon, may consist of various subprocesses, affected by various types of experience.

Superficially, imprinting in birds shares many characteristics with song learning; there being a sensitive phase for learning is but one of them. These similarities have led several people to categorize them together, for instance, as 'template learning' (Staddon 1983) or as 'programmed learning' (Gould 1982). This raises the question of how similar the underlying mechanisms are and, for species in which both occur, whether a direct linkage is present between the two. The species for which we know most about both processes is the Zebra Finch and Slater & Mann use this species to explore the links between the two processes. Among other things, they demonstrate that parental appearance may affect choice of a song tutor. Nevertheless the two processes are not inextricably linked. The benefit of comparisons of this type is that they give a better insight into what we know or don't know about the developmental mechanisms involved and this may help to reveal fundamental properties which may be of importance for understanding the development of other types of behaviour.

Sexual imprinting leads to a preference for some potential mates over others as a result of early experience. It has long been realized that, as a consequence of its effect on mate choice, imprinting may play a role in evolution and speciation. In my own

contribution I review the traditional views on this issue, which were based on the assumption that imprinting resulted in a preference for individuals which are most similar to the imprinting stimulus. Recent evidence, however, suggest that specific, deviating stimuli may be preferred over the familiar ones. I argue that this alters the evolutionary consequences of sexual imprinting. This contribution draws attention to the fact that theories regarding sexual selection and plumage evolution may benefit from giving attention to the proximate mechanisms underlying mate preferences and, in particular, to the role of experience in leading to specific preferences.

Imprinting is a subject which has featured prominently at a number of Ornithological Congresses, and much of the reason for this comes from the work of Konrad Lorenz and Klaus Immelmann. Both of them have died since the previous Congress at Ottawa (1986). As knowledge advances, cherished ideas may need to be abandoned or modified. The views expressed in this symposium may, therefore, differ from the ideas of these two pioneers. Nevertheless the contributions to this symposium testify to the impact these men had on imprinting research. We hope that the symposium will be seen as a tribute to, and an acknowledgement of, their intellectual legacy.

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DISPOSITIONS AND RECOGNITION IN IMPRINTING

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ABSTRACT. Imprinting in birds has provided some key insights into the way in which internal and external influences on behaviour interact. Young birds have strong dispositions to behave in particular ways but are greatly changed by their experience. When given an opportunity to choose between a conspicuous artificial imprinting object and a stuffed Jungle Fowl *Gallus gallus spadiceus*, naive chicks of Domestic Fowl prefer to approach the Jungle Fowl. Like other dispositions, the unlearned preference for particular features in the natural parent has a developmental history and a variety of different types of experience can change the rate at which it is expressed and under some circumstances it may not be expressed. Its expression does not require the same region of the brain as that involved in recognition of the familiar. Despite the neural separation, such is the interplay between the disposition and the recognition memory involved in imprinting in the intact bird that the effects of the two processes do not simply add together.

Keywords: Imprinting, dispositions, domestic chicks, recognition, sensitive periods.

INTRODUCTION

The capacities of young birds to show highly organised preferences and motor patterns and also to change their behaviour have both fascinated and teased generations of ornithologists. Many have written as if the different systems involved in development were identifiable in the final expression of the modified behaviour. The developmental processes giving rise to dispositions on the one hand and learning processes on the other have often been treated as though they were neatly separable in terms of the different forms of behaviour they supposedly produced, namely innate and learned components. Even though such a dichotomy of behaviour has been widely discredited, hope has lingered that simple links will be found between the starting points and the end-points of development. As a consequence, a pattern of behaviour is often referred to still as “genetic” or “acquired”. Despite such hopes, simple one-to-one correspondences between genes or experience and any network property of the nervous system or any patterning of behaviour do not seem at all plausible. Even though a certain gene or a certain event in the environment may be crucial for the expression of particular bits of behaviour, it would be very remarkable if that gene or that experience was all that was needed to determine the outcome. It is for these reasons that emphasis has been placed increasingly on the dynamics of what happens during the process of development (e.g. ten Cate 1989a).

A particularly interesting area in which the interplay between the developing bird and its environment has been worked out in some detail is the study of imprinting, first made famous by Lorenz (1935). Imprinting restricts the filial or social preferences to a particular class of companions (or inanimate objects) to which the young birds have been exposed at a particular stage. In some cases at least, the imprinting process can have profound and lasting effects on the sexual preferences of adults. It has been rewarding to study because learning occurs spontaneously. The interplay between

internal regulation and external conditions provides a beautiful example of how behaviour develops.

DISPOSITIONS TO RESPOND DIFFERENTIALLY

The birds which have been studied most intensively as far as filial imprinting is concerned, namely chicks of Domestic Fowl *Gallus gallus domesticus* L. and Mallard ducklings *Anas platyrhynchos* L., have relatively unstructured social preferences at hatching - which is why they can be induced to form attachments to ethologists. At one time, movement was regarded as essential in "releasing" the following response and hence in initiating the imprinting process. However, the effectiveness of the many visual stimuli used in imprinting depends on such properties as their size and shape, as well as on the angle they subtend to the bird and the intensity and wavelength of light they reflect. Moreover, the rates at which these variables change are also important - hence the undoubted effectiveness of movement and flicker.

The bird responds to a *pattern* of stimulation, and the most effective stimuli are clusters of features. Attention has been focused increasingly on stimulus features found in the natural world. Features of the Jungle Fowl *Gallus gallus spadiceus* Bonnaterrre, which is the ancestral form of the Domestic Fowl, are particularly attractive to chicks of Domestic Fowl (Horn & McCabe 1984). In this case, the preference for naturalistic stimuli had been missed for a long time because, under laboratory conditions, the necessary feature detectors seem to take longer to develop than do the ones driven by the flashing lights and movement and under certain conditions do not develop at all (Bolhuis et al. 1989a). Chicks of Domestic Fowl do not simply have a disposition to respond to the head and neck of Jungle Fowl. The head and neck of a duck or even a small mammal turned out to be just as effective (Johnson & Horn 1988).

NEURAL SEPARATION OF DISPOSITIONS AND RECOGNITION

Neural analysis of imprinting has strongly suggested that particular parts of the brain are concerned with storing representations of the familiar companion (or inanimate imprinting object). The work which led to this conclusion has been reviewed many times (e.g. Horn 1985, 1991) and will not be described in detail here. One of the key sites lies in the intermediate and medial part of the hyperstriatum ventrale (abbreviated as IMHV) on the left side of the brain. Johnson & Horn (1987) found that, while intact chicks of Domestic Fowl were able to discriminate between a familiar stuffed adult Jungle Fowl and a novel one, those with bilateral IMHV lesions could not do so. In a study of mate choice, Bolhuis et al. (1989b) found that adult female Domestic Fowl with bilateral IMHV lesions placed shortly after hatching responded equally to familiar and novel males of the same breed as well as to novel males of a different breed. In contrast, intact birds significantly preferred males slightly different but not too different from the ones with which they had grown up, as had proved to be the case with Japanese Quail *Coturnix coturnix japonica* (see Bateson 1988).

The development of the disposition to respond to objects with head and neck features does *not* depend on IMHV (Horn 1985, 1991). Therefore, the neural analysis has dissociated the underlying structures involved in recognition from those involved in the

development of the disposition. On the face of it, these findings might seem to support the old view that behaviour can be broken up into learned and unlearned components. Furthermore, some behavioural evidence appears at first sight to lend support to the idea that the effects of the dispositions and the learning process add together (Bateson 1978). However, the behaviour of the whole animal is very unlikely to be the additive product of the various subprocesses that are required for the bird to function properly. Furthermore, many other factors besides dispositions and a capacity to recognise familiar objects affect the young bird's behaviour.

INTERACTION OF THE FACTORS INFLUENCING IMPRINTING

Despite the spontaneity of imprinting, it has been obvious for a long time that the results of an imprinting experiment depended greatly on the conditions that were used. Imprinting with a novel and conspicuous object usually occurs most readily at a particular stage in development, known as a sensitive period (e.g. Bateson 1979). Many factors have relatively short-term effects on responsiveness and much research has been devoted to sorting them out. For example, Polt & Hess (1966) found that chicks of Domestic Fowl given two hours of social experience with siblings beforehand followed a moving object more strongly than isolated birds (see also Lickliter & Gottlieb 1988). Stimulation in other modalities, when presented concurrently with visual stimuli, can have a powerful facilitating effect. In forming a social attachment under natural conditions, auditory signals are very important in guiding the process (see Dyer, this symposium). Nonetheless, studies of imprinting provide unambiguous evidence for the formation of visual stimulus representations. The visual image is not only retained for a long period of time in the case of sexual imprinting, but also in the case of filial imprinting the details held in memory are remarkably specific, enabling the subsequent identification of individuals (e.g. Johnson & Horn 1987). Objects with certain features probably have a positive effect on state since the behaviour of a live adult female has a facilitating effect on the response to her by Japanese Quail chicks (ten Cate 1989b). The range of objects which enable, facilitate and elicit social behaviour is restricted by the animal's experience. Thus, when the young bird becomes familiar with one object, the likelihood of it withdrawing from dissimilar conspicuous objects increases. The so-called sensitive period seems to be brought to an end by the formation of a social attachment (Bateson 1979).

MODELS OF IMPRINTING

The importance of developmental stage, motivational state and the active role of the animal in the process have been incorporated into a theoretical scheme (see Bateson 1991). As a bird reaches a particular stage in development, the system which controls searching is activated. The searching may bring the animal into contact with an object that has features to which it is predisposed to respond. The object's features drive the executive system controlling approach. Simultaneously, searching is inhibited. At an early stage in the process the recognition system is addressed but nothing has yet been stored there. When the bird is more experienced, a familiar object matches its representation in the recognition system, which by now exclusively controls approach movements. Finally, when a bird encounters a strange object, its features fail to match the representation of the familiar object and so the bird withdraws. In the presence of a familiar object, of course, withdrawal is inhibited.

In the present context of focusing on dispositions and recognition memory, the way of thinking about imprinting outlined above helps to separate factors that are likely to influence motivational state or are peculiarities of the context in which this particular form of recognition learning takes place. The crucial part of this approach that deals with the storage of visual information is shown in Figure 1 and involves three stages: analysis, recognition and execution (see Bateson 1990,1991).

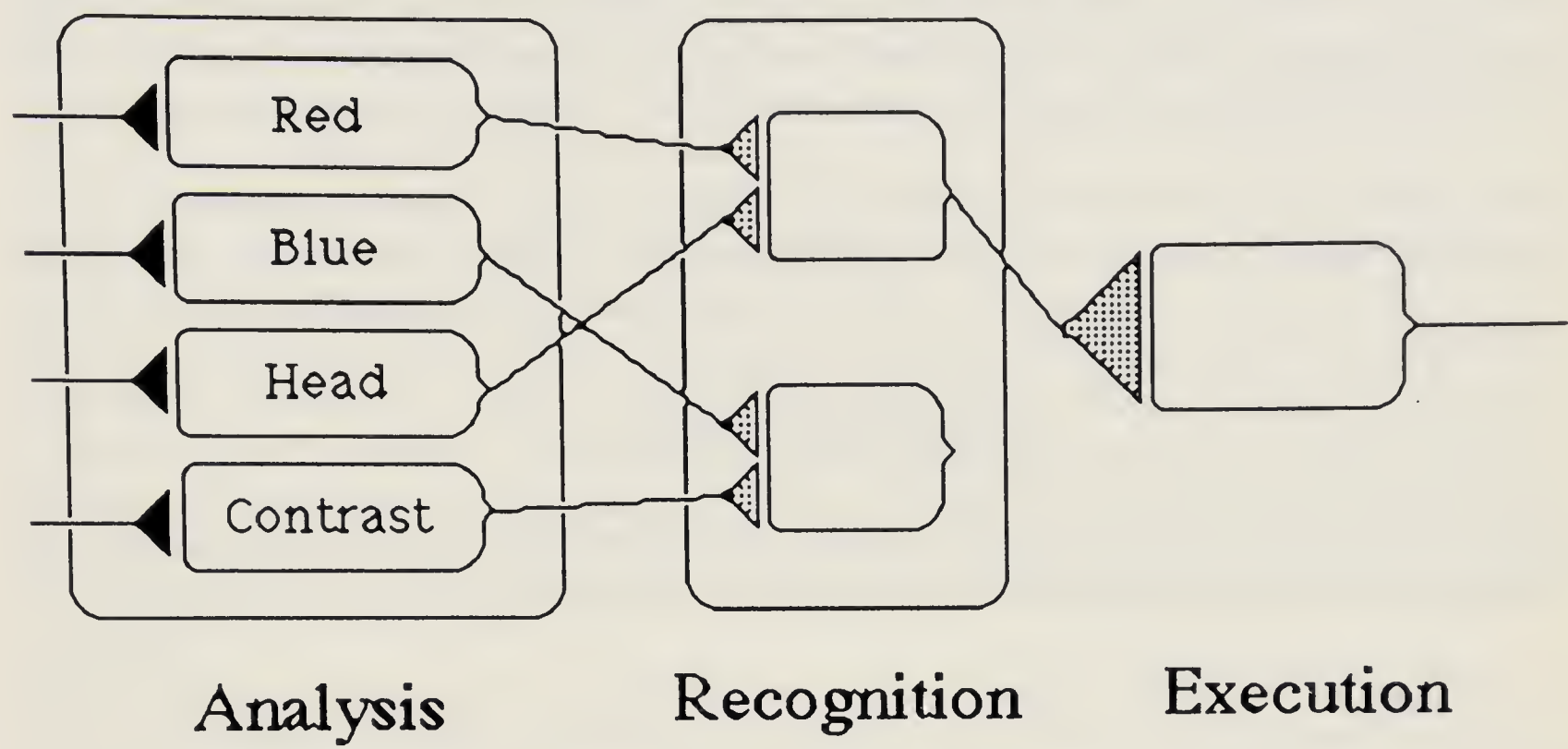


FIGURE 1 – A simple scheme of the stages from input to output involved in filial responses to a mother hen or a substitute imprinting object. Only some of the feature detectors thought to exist in the analysing system are shown. Plasticity resulting from imprinting occurs both where the feature detectors connect with the recognition system and where the output from a given representation connects to the executive system controlling filial behaviour. Another representation of an object to which the bird is tame is also shown. This does not have access to the executive system because all available connections have been captured by the first. This partial version of a model described more fully in Bateson (1991) does not include direct control of the executive system by the analysing system.

The dispositions derive from the various feature detectors which develop independently of the storage of the representation of a familiar object. Only some of the feature detectors are shown addressing the recognition system in Figure 1. Each of the feature detectors is connected to each of a population of neurones in the recognition system and, at least in a subset of those neurones, the particular connections that had been active during imprinting are strengthened. The strengthened connections between the analysis and recognition systems subsequently constitute the representation of the imprinting object.

The final step in the proposed process is the establishment of a link between the representation of the imprinting object and the executive system controlling social behaviour. The first preferences to be formed are likely to be the ones that last, within certain constraints such as the age of the animal at its first exposure and the length of that exposure (e.g. Bolhuis & Bateson 1990). When a bird is well imprinted, it can be exposed to another object. At first the bird withdraws, showing every sign of great alarm. By degrees this alarm habituates and the bird becomes tame. However, tame birds do not necessarily express any social behaviour towards the object which is by now very familiar. They evidently recognise it, but that is all. These results led to the

speculation that two forms of neural change might be involved, one concerned with recognition of previously experienced inputs and another concerned with connecting up the mechanism involved in recognition of familiar inputs to the execution of filial or, later in life, sexual behaviour (Bateson 1981).

Suppose that gaining access involves growth of neural connections and that the area available for connections has finite size. When growth has proceeded beyond the half-way point and cannot be reversed easily, the input experienced first will be better able to control the behaviour than other forms of input - a form of competitive exclusion.

In the case of sexual imprinting, the final hook-up between the representation of the imprinting object stored in early life and the executive system controlling sexual behaviour probably does not occur until much later than original storage of the representation (see Kruijt, this symposium). Prolonged exposure to one individual, with which the young bird becomes familiar, followed by exposure to a second individual can still lead to a sexual preference for the second (see Bateson 1979). Delay in hooking up to the executive system for sexual imprinting makes good biological sense. It allows the bird's sexual preferences to be affected by the appearance of siblings when they are adult-like as well as by the appearance of their parents.

To summarise the view of imprinting presented here, the recognition mechanisms have large capacities for storing representations of different objects. Once change has occurred here, further changes are made more difficult by escape from all novel objects. However, when escape from a particular object has waned, its characteristics can also be represented in the recognition system as a result of further exposure. By contrast the possibilities for accepting new connections into the executive system are limited. The capacity for plastic change here is believed to be severely restricted. Once this capacity is used up, the animal may become tame to a novel object, but will not respond to it socially.

A conclusion from my attempts to formalise the models of imprinting (Bateson 1991) is important. I could not develop equations that simply involved additive interplay between the major terms. This was because, when dealing, for example, with the interaction between the attractiveness of an object and the bird's readiness to respond, if either had a zero value, nothing should happen. If the model were additive, a bird that was not ready to imprint would, nevertheless, learn the characteristics of things and birds that were not ready for imprinting would appear to learn in the absence of anything to learn about. To avoid such pitfalls, the model had to be multiplicative. Furthermore, the effects of experience on the behaviour of a real bird are not likely to be linear.

Despite the multiplication involved in the equations, it was interesting that, within a limited range of parameters, the results of the simulations seemed to suggest that the effects of imprinting did add on to the effects of the dispositions (Bateson 1991). As I have already noted this is also true with real animals. So it is possible to generate data which, in the case of those produced by the model, appear to support an erroneous conclusion.

CONCLUSION

The work on imprinting has drawn attention to the advantage of separating motivational state, stimulus analysis, the capacity for plastic change and the executive control of behaviour. The work has shown how it is necessary to postulate features of the organism that have developed before the stage in which one is interested and also how subsequent development depends on current conditions external to the organism. The old either/or oppositions applied to behaviour simply evaporated when knowledge started to advance. The nature of the processes seems straightforward, but it is exceedingly difficult to see how they could possibly be additive. Even so, the regularities of development were almost certainly fine-tuned to the conditions in which the animals evolved. Therefore, species differences in patterns of development are likely to be ubiquitous.

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A SOCIAL PERSPECTIVE ON IMPRINTING: THE ROLE OF SIBLINGS IN THE ESTABLISHMENT OF MATERNAL ATTACHMENT

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ABSTRACT. For over 50 years, researchers reported that visual characteristics of imprinting stimuli mediate the maternal imprinting process. These investigations used artificial stimuli and social isolation which were incongruent with the hatchling's species-typical environment. Research approximating the natural environment by using naturalistic stimuli and social rearing with siblings showed that ducklings do not exhibit a visually imprinted maternal preference if siblings are one of the choices in the test situation or if siblings are present during maternal imprinting. Sibling presence during maternal imprinting disrupts a visual preference for the hen but does not affect the preference for the maternal call. Ducklings preferred the maternal call regardless of the hen's visual characteristics. Thus, *early* in development, the attractiveness of the hen's assembly call is dominant over her visual characteristics in maternal imprinting and allows for individual auditory recognition of her in nature.

Keywords: Maternal imprinting, peer imprinting, social attachments, Mallard ducklings, *Anas platyrhynchos*.

INTRODUCTION

Lorenz (1935, 1937) termed the imprinting process as 'Pragung' (translated literally as 'stamping' or 'coining'). He characterised this as a rapid and irreversible (i.e. not forgotten or modifiable) process by which a young precocial bird develops a social preference for a particular individual or object it encounters soon after hatching. This leads it to prefer and restrict its social behaviour toward conspecifics. Lorenz also hypothesized that the young bird establishes a functionally distinct social companion or 'Kumpan' for each of its social activities during development. Explicit in Lorenz's account of imprinting was that parents (only the hen is present for some species) and siblings are *both* important in the establishment of species-typical social preferences.

The early social attachment between the hatchling and its hen is assumed to be a result of a visual imprinting process by which the hatchling learns the specific visual characteristics of its hen during a brief exposure to her (Bateson 1966, Hess 1959, Sluckin 1973). Since the 1950s, most of the imprinting research has been conducted in the laboratory, with little regard for the natural ecological and social context of the subjects. For an exception, see Hess (1973). For example, investigations of imprinting have typically used highly artificial stimuli as maternal surrogates, which include flashing lights, coloured balls or boxes, and balloons. These studies showed that isolate-reared ducklings *Anas platyrhynchos** and chicks *Gallus gallus domesticus* quickly acquire preferences for these unnatural objects. Recent research (Johnston & Gottlieb 1981), however, revealed that the use of natural stimuli such as stuffed replicas of hens of different species, with subtle differences, diminishes the ease with which ducklings exhibit visual preferences. As shown in Table 1, isolate-reared

* Common and scientific names follow AOU (1983).

Mallard ducklings that were imprinted to a vocal Mallard hen model were able to discriminate between the familiar stuffed Mallard hen and a Pintail hen *Anas acuta* but were unable to discriminate between the Mallard hen and a Redhead hen *Aythya americana*. This finding suggests that ducklings find it difficult to discriminate between the visual characteristics of their own and related species and perhaps find it more difficult to recognize the visual characteristics of their individual mother which is assumed to occur in maternal imprinting. Further, characteristics other than the hen's visual cues, such as her vocalisations, have been neglected despite reports that the hen's vocalisations may be more important in determining the hatchling's attachment to her than her visual appearance (Bailey & Ralph 1975; Bjarvall 1967, Gottlieb 1966, 1971, Miller & Gottlieb 1978, Impekoven 1976).

The species-typical social context of maternal imprinting has also been neglected in most laboratory investigations as subjects are generally reared in social isolation. However, sibling isolation is in marked contrast to the social context of imprinting as it occurs in nature. In the natural environment, the context in which Mallard ducklings become imprinted is a highly social one in which the hatchling receives stimulation from its siblings as well as from its hen (Collias & Collias 1956, Joyner 1977). As a result of isolation rearing, the use of easily discriminable maternal surrogates, and the neglect of other species-typical stimulation such as maternal vocalisations, it comes as no surprise that many researchers have assumed filial imprinting to be mediated primarily by the hen's visual characteristics. Below, I will first review the evidence which shows that social experience with siblings, in some cases, enhances maternal visual imprinting, and next, I will present evidence which demonstrates that experience with siblings interferes with maternal visual imprinting. Lastly, I will show that in the context of social rearing, maternal vocalisations are prepotent over the hen's visual characteristics in attracting the brood to her while siblings visually imprint on each other.

SIBLING INFLUENCE ON MATERNAL VISUAL IMPRINTING

Enhancement of maternal visual imprinting

Since 1981, Gottlieb and his colleagues have investigated the imprinting process within the species-typical context of sibling interactions. In some cases, they found that interaction with siblings enhances maternal visual imprinting (Johnston & Gottlieb 1981, 1985, Lickliter & Gottlieb 1985, 1987, 1988). In these studies, domestic Mallard ducklings were each allowed to follow a natural stuffed model of a Mallard hen which emitted a recording of the Mallard maternal assembly call (details of the calls in Miller & Gottlieb 1978). Following the imprinting training trial, ducklings were tested individually for their visual preference for the silent familiar Mallard hen or a silent unfamiliar Redhead hen (Table 1). Ducklings reared in isolation (Johnston & Gottlieb 1985) and ducklings that received social experience with broodmates *before* but not after imprinting (Lickliter & Gottlieb 1987) were unable to make this difficult visual discrimination. However, as Lickliter & Gottlieb (1985) showed, social rearing with broodmates *following* maternal imprinting enabled the ducklings to exhibit a visual preference for the familiar Mallard hen over an unfamiliar Redhead hen. This effect is species-specific in that rearing a Mallard duckling with other species such as domestic chicks or Muscovy *Cairina moschata* ducklings does not produce a visual preference for the Mallard hen (Lickliter & Gottlieb 1988).

TABLE 1 - Preference of ducklings for the visual characteristics of the familiar Mallard hen and an unfamiliar hen of a different species in a simultaneous choice test 48 hours after hatching. The conditions above the broken line are from Johnston & Gottlieb (1981); conditions below the line are from Lickliter & Gottlieb (1985, 1987).

Rearing Condition	Preference Test	Preference*
Reared in isolation from hatch to testing	Mallard vs. Pintail	Mallard
Reared in isolation from hatch to testing	Mallard vs. Redhead	No preference
Reared in isolation from hatch to testing	Mallard vs. Redhead	No preference
Reared in social group from hatch to training; isolation from training to testing	Mallard vs. Redhead	No preference
Reared in isolation from hatch to training; social rearing from training to testing	Mallard vs. Redhead	Mallard

* Preference was assessed using the binomial test, $P < 0.01$.

Interference of maternal visual imprinting

Further studies (Lickliter & Gottlieb 1986a, 1986b; Dyer et al. 1989) showed that social interaction with siblings interferes with the display of a visual maternal preference if siblings are one of the choices in the test situation. This interference is thought to be due to “peer imprinting,” whereby ducklings imprint to their broodmates during the social rearing experience. Lickliter & Gottlieb (1986a) reported that social rearing with siblings redirects the visually imprinted maternal preference from the stuffed hen model to stuffed natural models of siblings. In that study, following training with a vocal stuffed Mallard hen, ducklings were tested for their visual preference for the silent Mallard hen or for silent stuffed siblings. A visual preference for the Mallard hen over the stuffed ducklings occurred only if ducklings were reared in social isolation for the duration of the experiment. To control for the possibility that the preference found for ducklings was due to a greater amount of exposure to siblings than to the hen, the hen was placed in the social rearing enclosure for 72 hours prior to testing. This prolonged exposure to her did not produce a visual preference for her and did not reduce the ducklings' preference for their siblings.

The previous study shows that peer imprinting can disrupt maternal visual imprinting. However, one obvious possibility for the ineffectiveness of the hen may be the noninteractive nature of the stuffed hen as compared with the interactive nature of live ducklings. Dyer et al. (1989) found that peer imprinting occurred with individual ducklings reared for 48 hours in a brood situation with live ducklings. Furthermore, and more importantly, peer imprinting occurred for ducklings reared individually with seven noninteractive stuffed broodmates. These ducklings were never exposed to live

siblings. Lastly, ducklings did not show a preference for the hen or stuffed siblings when peer imprinting was prevented by rearing the ducklings individually with her for 48 hours. These results demonstrate that minimal experience with siblings, even noninteractive siblings, is sufficient for the induction of a visual preference for broodmates. Thus, the hen's lack of visual attractiveness was not due to her inanimate nature alone since exposure to inanimate stuffed siblings was effective in producing a visual preference for them in testing. However, a possibility remains that ducklings might respond differently if a live, silent hen and live siblings were used.

Further, Lickliter & Gottlieb (1986b) found that the presence of broodmates *during* maternal imprinting disrupted the acquisition of a visual preference for the familiar Mallard hen. Ducklings that were trained (imprinted) in broods of four did not show a visual preference for the familiar Mallard hen, over an unfamiliar Pintail hen when tested individually. Isolate-reared and individually-trained ducklings can make this discrimination. Group-trained (but otherwise socially isolated) ducklings showed a preference for stuffed siblings over the familiar Mallard hen which indicates that peer imprinting had occurred during the training trial and that it interfered with maternal visual imprinting. Taken together, these studies suggest that ducklings find the visual characteristics of their siblings more attractive than the visual characteristics of their hen. Since imprinting in nature occurs with both the hen and broodmates present, factors other than her visual characteristics may determine the ducklings' attachment to her early in development. One such factor that may influence ducklings' attachment to their hen is the hen's maternal vocalisations (i.e. her assembly call).

SIBLING INFLUENCE ON THE AUDITORY BASIS OF MATERNAL IMPRINTING

One commonly overlooked source of stimulation in laboratory analyses of maternal imprinting is the hen's species-specific maternal vocalisations. Field observations (Ramsay 1951, Collias & Collias 1956, Bjarvall 1967, Miller & Gottlieb 1978) consistently report that the hen's maternal calls are more important than her visual appearance in eliciting the approach and following behaviours of her brood. Miller & Gottlieb (1978) observed that Mallard hens begin to vocalise at about the 17th day of incubation and will continue to utter these maternal calls throughout the hatching and brooding period of their young. The hen's vocalisations generally become more intense at the time of the initial exodus from the nest site. Often, the hen must make several attempts to entice her brood to follow her from the nest and, during these attempts, the hen emits the maternal call (Bjarvall 1967). Earlier work by Gottlieb (1968, 1971) revealed that hatchlings show a preference for the species-specific maternal vocalisations even if these young birds have not had prior exposure to the hen's call. The young of other species, including Ring-necked Pheasants *Phasianus colchicus* (Bailey & Ralph 1975), Ring-billed Gulls *Larus delawarensis* (Evans 1973), White-rock chicks *Gallus gallus domesticus* (Gottlieb 1971), and Bobwhite Quail *Colinus virginianus* (Heaton et al. 1978) also exhibit a selective preference for species-specific vocalisations.

Maternal vocalisations may be the means for species identification and individual recognition. According to Miller and Gottlieb (1978), species-typical vocalisations have general features in common which may provide the basis for species identification. These vocalisations also vary in repetition rate and frequency spectrum across

individual hens. The repetition rate and spectral variability in intraspecific vocalisations among individual hens may be the basis for the hatchlings' recognition of their individual hen in nature (Miller & Gottlieb 1978). For example, Kent (1978) found that domestic bantam chicks preferred the clucks of their hen over an unfamiliar hen but that the preference diminished if the chicks were separated from their hen for a period of four hours. Gottlieb (1988) reported that Mallard ducklings were able to learn the characteristics of a specific Mallard hen's assembly call and when tested 30 hours later, showed a preference for that familiar call over an unfamiliar Mallard's assembly call. Surprisingly, these hatchlings learned the specific Mallard call with only 12 minutes of exposure to that call during the first 24 hours after hatching. These results indicate that Mallard ducklings are capable of learning the individual characteristics of their hen's vocalisations and thus should be able to identify her by her vocalisations even if they cannot identify her by her visual appearance.

If the maternal vocalisations are the basis of maternal imprinting, these calls should override the attractiveness of siblings that are present in the training and testing situation. In a study by Dyer & Gottlieb (1990), socially-reared domestic Mallard ducklings were imprinted in broods of four to a vocal Mallard model and then were tested in broods for their visual preference for the silent familiar Mallard and a silent unfamiliar Pintail hen. As with the results reported by Lickliter & Gottlieb (1986b), the broods showed no preference for the visual characteristics of either model. However, when the Mallard and Pintail maternal calls were present in the test situation, the broods overwhelmingly chose the Mallard call over the Pintail maternal call *regardless* of whether the Mallard call emanated from the visually familiar Mallard hen or the visually unfamiliar Pintail hen. Earlier observations recorded by Lorenz (1935) while he was a surrogate mother to three Mallard ducklings and six Mallard x 'Hochbrutente' ducklings support the finding that the maternal call is prepotent over the hen's visual characteristics for Mallard ducklings. Specifically he reported:

The progress of the experiment demonstrated that the maternal call is very probably the decisive character of the maternal companion for the mallard and that the appearance of the companion is individually imprinted:

At first, I was unable to stop quacking, since the ducklings would otherwise soon start to utter lost piping. Only when the ducklings were older was I recognized as the maternal companion even whilst I was silent. Thus, one can extricate in individual cases the property which the maternal companion must without exception possess, and which of her characters are imprinted on the young bird only in the course of ontogeny (Lorenz, 1970, page 139).

Taken together, these observations suggest that the maternal call can override the attractiveness of siblings and is perhaps the initial determining factor in the establishment of a maternal preference early in the duckling's development. Recent research (Bolhuis et al. 1985, Johnson et al. 1985, Johnson & Horn 1988), however, reveals that domestic chicks prefer complex/naturalistic visual stimuli over less complex/artificial stimuli. This emerging general preference (Bateson, this symposium) may serve to make siblings more visually attractive and thus promote peer imprinting. Although Johnson & Horn (1987) found that domestic chicks reared in social isolation were able to visually discriminate between two hens of the same species, it remains to be shown that visual recognition of individual hens occurs within the context of social rearing with siblings as it would occur in nature.

CONCLUSIONS

In the natural environment, maternal imprinting occurs within the context of sibling interactions. When the naturally occurring social context of maternal imprinting is taken into account, socially reared ducklings imprinted and tested in broods respond to the species-specific maternal vocalisations and show no preference for the visual characteristics of their hen. Interestingly, Bossema & Kruijt (1982) have shown that adult male Mallard ducks do respond to the visual characteristics of female Mallards of different colour strains following rearing experience with these strains. Therefore, the development of visual preferences for particular colour phenotypes does occur during development. Additionally, ten Cate (1989) found that Japanese Quail chicks *Coturnix coturnix japonica* show stronger attachments to a living hen when compared with chicks exposed to a moving natural model of a hen. Chicks exposed to a non-moving model did not exhibit any evidence of attachment to the model. However, the question remains as to when in development the young learn the visual features of the hen. It is possible that the vocalisations of the hen in combination with her behaviour increases the probability that her brood will learn her specific visual characteristics. It is also likely that the hen's behaviour in combination with her vocalisations serve to make her an attractive stimulus that can override the siblings' strong attachment to each other. However, the selective responsiveness of young birds to maternal species-specific vocalisations and the lack of such specificity for the visual characteristics of the hen points to the overall dominance of species-specific auditory stimulation in the maternal imprinting process. It seems reasonable to conclude that the early development of maternal attachment is first determined through the auditory modality and perhaps only later supported or maintained through the addition of the visual characteristics of the hen.

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THE POSSIBLE ROLE OF COURTSHIP EXPERIENCE IN THE CONSOLIDATION OF SEXUAL PREFERENCES IN ZEBRA FINCH MALES

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ABSTRACT. Recent research on sexual imprinting is directed at gathering empirical evidence which throws light on the process underlying the development of sexual preferences, rather than highlighting the uniqueness of imprinting, which was emphasized in earlier research. One of the unique traits was the presumed irreversibility of imprinting. Recent findings, however, question the generality of irreversibility of the effects of early experience on sexual preferences: sexual preference of adult male Zebra Finches *Taeniopygia guttata castanotis* can be modified as a result of exposure to another species than the one by which they were reared. Under experimental circumstances, the extent to which this occurs is dependent on whether the adult male has been exposed to a female of the rearing species. If this has been the case, the sexual preference is more difficult to modify.

Keywords: Zebra Finch, sexual imprinting, irreversibility, stability, sensitive period, sexual behaviour, courtship.

INTRODUCTION

Ever since Lorenz (1935), the development of social attachments has been a favourite subject for ornithologists. This was undoubtedly partly due to his broad generalisations: imprinting was considered to be a process that was different from learning processes that were being studied by animal psychologists at the time. The unique properties of imprinting according to Lorenz are well known: the rapidity of the process, restriction to a short sensitive period early in life, irreversibility, and lack of dependence on rewards as in conditioning. For many years research was concerned mainly with evaluating whether these criteria indeed applied to imprinting. Thus, the emphasis of many studies was on classification, rather than on analysing imprinting as a process. Fortunately, recent research is changing in this respect (e.g. ten Cate 1989). The present paper is concerned with sexual imprinting, a subject that has received little attention compared with filial imprinting, due to the much longer period of development that is involved. In our laboratory we have followed the lead of the pioneering research by Immelmann with Zebra Finches *Taeniopygia guttata castanotis*. In our studies we have analysed aspects of the behavioural situation in which imprinting occurs, in the expectation that this will add to our insight in the nature of the underlying process (see Kruijt 1985 for a review). For example, by analysing the social context to which the young bird is exposed, ten Cate (1982, 1984, ten Cate et al. 1984) has shown that conspecific parents are more effective as imprinting stimuli than Bengalese Finch *Lonchura striata* foster parents. This can be explained in part by more social interactions that are occurring with conspecifics compared with Bengalese Finch foster parents, e.g. feeding. Similarly, social experience with siblings plays a role in the process (ten Cate 1982, Kruijt et al. 1983). These findings are in contrast to the view held for a long time by many that imprinting occurs as a result of mere passive exposure. In the present paper I shall report results concerned with the presumed irreversibility of sexual imprinting in Zebra Finches.

IS SEXUAL IMPRINTING IRREVERSIBLE?

Lorenz (1935) suggested a strong version of irreversibility of imprinting: once an attachment was formed, sexual and other social responses were not shown to individuals of another species than the one imprinted upon. As an example he reported that birds imprinted on humans, would not be interested in conspecifics, even if they were kept together for years in the absence of contact with humans. When subsequently confronted with humans they still directed their species-specific social behaviour to humans only. In contrast, Immelmann (1972) found that male Zebra Finches cross-fostered by Bengalese Finches preferred Bengalese Finch females in choice tests, but could also direct sexual behaviour toward, and even breed successfully with, females of their own species if kept together for a prolonged time in the absence of Bengalese Finches. However, in subsequent choice tests, these males immediately preferred Bengalese Finches as strongly as before. Therefore Immelmann concluded that Lorenz's claim regarding the irreversibility of imprinting (as well as the other criteria distinguishing imprinting from conventional learning processes) is fully realized in the case of sexual imprinting in Zebra Finch males, and estimated that the sensitive period ended at the age of about 40 days. However, this position was modified as a result of subsequent findings. These showed, first, that cross-fostered Zebra Finch males could be re-imprinted on their own species by giving them intra-specific experience in the adolescent phase, i.e. after 40 days and up to the age of about 70 days, long after the age that was originally postulated as the end of the sensitive period (Immelmann 1979, 1985, Immelmann & Suomi 1981). In the same papers the conclusions regarding the effects of breeding experience with conspecifics were also changed, although it was still maintained that re-imprinting was not possible in adult cross-fostered males. Immelmann noted (e.g. Immelmann 1979, p.123) that about 20% of cross-fostered Zebra Finch males that received breeding experience with a conspecific female showed a transient preference for Zebra Finch over Bengalese Finch females. This preference disappeared within days or at most within several weeks, and was replaced by a preference for Bengalese Finches. Because the reversal to a preference for conspecifics was temporary, and the initial preference emerged again and was then thought to be retained indefinitely, Immelmann continued to hold the view that sexual imprinting was irreversible.

At the same time Bischof (1979) published a theoretical paper, in which unpublished findings by Immelmann were discussed briefly. These led Bischof to the conclusion that the return to a preference for Bengalese Finches occurred in males that had been given choice tests before breeding with a conspecific female. On the other hand, males that had not been previously tested preferred Zebra Finches subsequently, and for these males a return to the original preference for Bengalese Finch females in subsequent tests was not reported. As mentioned by Bischof, this could imply that, apart from early experience with foster parents, adult experience, perhaps courtship in choice tests, might also play a role in the final determination of sexual preferences.

Bischof (1979) did not provide details of experimental data, nor was the subject mentioned in the later papers by Immelmann. Yet, if the described differences were real, they would throw new light on the processes underlying the development of sexual preferences. Another reason to tackle this problem was that I realized that, in ontogenetic studies, we usually manipulate the amount and nature of experience and then test for differences in the effects, but we usually take it for granted that such tests

merely reveal the effects of previous experience and do not by themselves have influence on the developmental process. However, this is a hidden supposition that is rarely explicitly verified. Below I will discuss experiments which have subsequently been carried out on the issue, both by Immelmann et al. (in press) and ourselves (Kruijt & Meeuwissen in press).

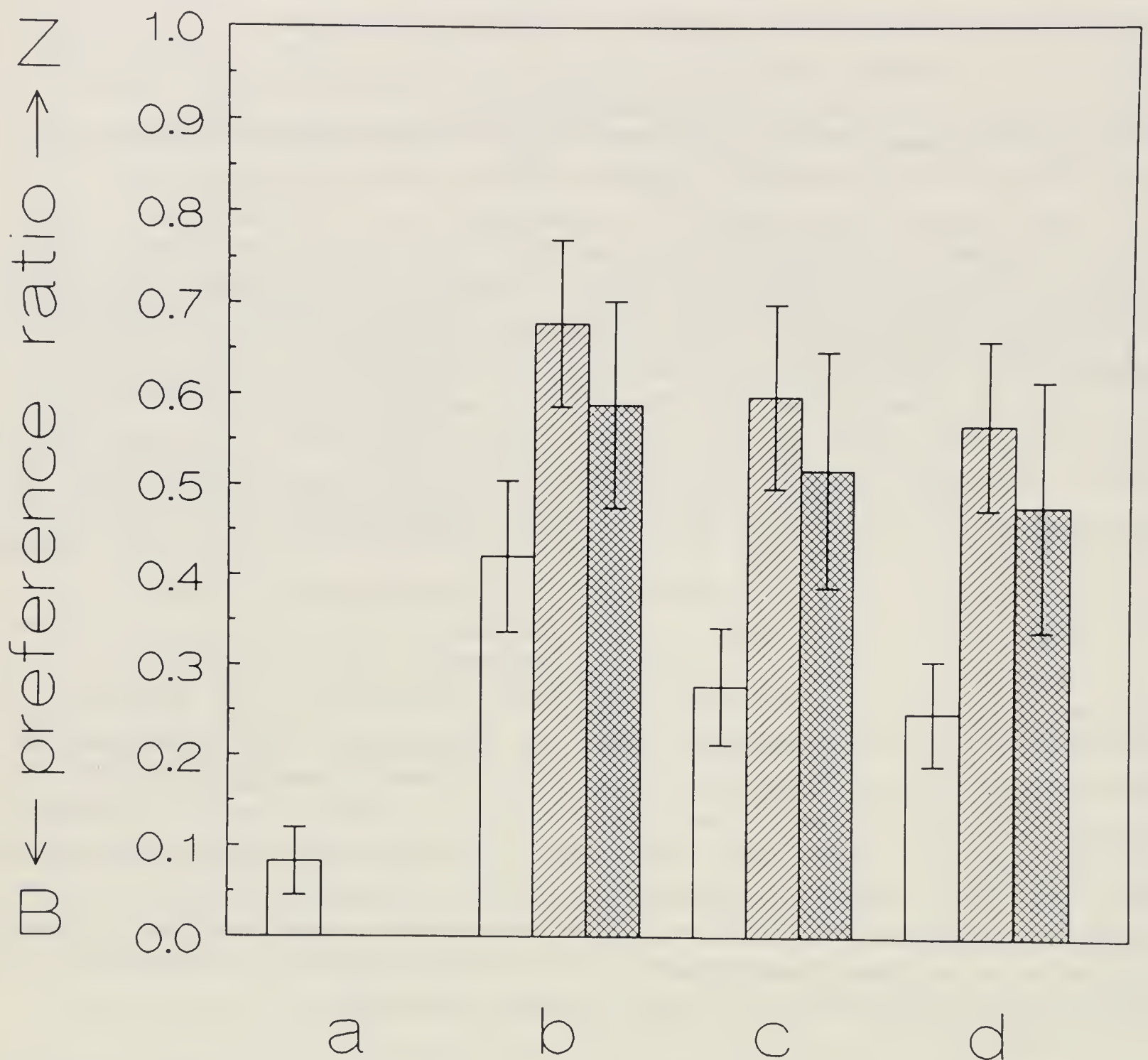


FIGURE 1 – Average preferences \pm SE of cross-fostered Zebra Finch males in four series of choice tests between a Zebra Finch and a Bengalese Finch female. Preference ratio: number of song strophes to the Zebra Finch female divided by total number of song strophes, for each male averaged over three tests per series. Series a: weekly tests between 100 and 120 days; b: weekly tests between 220 days and 235 days; c: monthly tests between 260 and 325 days; d: 3-monthly tests between 410 and 590 days. Open and striped columns: exposure to conspecific female with breeding experience; hatched columns: exposure to conspecific female with separation by wire (non-tactile experience).

EFFECTS OF EARLY AND ADULT EXPERIENCE

The possibility that sexual preferences can still be altered in adult Zebra Finch males was investigated as follows (for more details, see Kruijt & Meeuwissen in press). Young male Zebra Finches were transferred to and reared by Bengalese Finch parents, separated from their parents at 40 days and isolated individually in a room where

they could hear but not see other Zebra Finches. Between 100 and 120 days, some of the males were submitted individually to three choice tests of 30 min, in which they could direct courtship and song from a central cage to a Zebra Finch female and a Bengalese Finch female located in cages on either side. On average, these males had a 8% preference for the Zebra Finch, expressed as the relative frequency of directed song. The other males remained in isolation and so obtained no opportunity to court or sing towards Bengalese Finches. Next, all males were given experience with conspecific females. This was done by putting each male in a cage with a nestbox and a conspecific female, where they stayed for three months from 120 days onwards. Subsequently, over a period of more than one year, each male's preference was determined again in nine choice tests, and mean preferences for each series of three tests were calculated.

As shown in Figure 1, after the period of exposure to a conspecific female, males of both groups showed, on average, a strong shift in preference towards a more Zebra Finch directed preference. Furthermore, those males that had been subjected to choice tests prior to the exposure period showed a significantly smaller shift than the males that did not receive these tests. At the individual level, the results were similar: 40% of the males with prior choice tests showed a significant preference for Zebra Finch females in the first series of choice tests after breeding and this was the case for 65% of the males without choice tests before exposure. So, both choice tests and subsequent exposure to a conspecific female affect the sexual preference. Similar findings have been obtained by Immelmann et al. (in press).

In both groups of males there was great inter-individual variation in the amount by which preferences were shifted in the direction of the Zebra Finch female, as well as in the number of fledglings that were produced by the pairs during the breeding period. A positive effect of breeding success on the amounts of shift might have been expected, but this relationship was absent.

So, the question arises as to what other experience during the breeding period may have been responsible for the alteration of sexual preferences. In choice tests given before exposure to the conspecific female, males preferred Bengalese Finches strongly: almost all their courtship and song were directed to the foster species. These males showed a smaller shift to Zebra Finch directed courtship after exposure to the conspecific female than did males without prior exposure. It could be hypothesised that exposure to a female in a sexual context, rather than the tactile contacts which occur during the period of breeding with the female, affects the sexual preference.

To examine this hypothesis, a third group of cross-fostered Zebra Finch males was exposed for three months to a conspecific female, separated from her by double wire. So the male could see the female, courtship and song could be performed, but tactile contacts such as occur in the breeding situation were impossible. These males did not receive prior choice tests. The shift in preference after the exposure is somewhat, but not significantly, smaller than in males that had breeding contact without prior choice tests (Figure 1). So, tactile contacts were not essential to give rise to a shift in preference.

A possibility to interpret this finding is that the consolidation of the preference developed earlier occurs if exposure is to the rearing species, as was also suggested by Bischof (1979). On the other hand, exposure can lead to a new preference, for the conspecific female, if this occurred before exposure to the rearing species. It can also

be concluded that exposure to the rearing species diminishes the capacity of males to modify their preference, if exposed to a female of another species in a sexual context. So, it seems that both types of experience oppose each other.

The effects of exposure of adult males to a female in a sexual context are remarkably stable. Although the shift in preference to the Zebra Finch female declines significantly in all groups, the effects of both consolidation and modification remain present for more than one year afterwards.

How can the strong effects of exposure in a sexual context be explained? One way to look at this question is to suppose that exposure in a sexual context has physiological effects: e.g. the male's perception of the female and, possibly, her sexual invitations, or the performance of courtship and song by the male, could lead to hormonal secretions in the male, e.g. testosterone, as a result of which the sexual preference that developed earlier is consolidated or modified. This possibility is at present being examined in our laboratory.

Another way to look at it is to relate the results to a model proposed by Bateson (1981) which describes two stages of processing of information in imprinting: first, incorporation of information in a recognition system, and second, access of this system to the executive system(s) controlling filial and sexual behaviour. Bateson initially developed this model for filial imprinting and emphasised duration of exposure as a factor influencing linkage of the recognition system to executive system(s), and duration of time since exposure as a factor which inactivates the links. It seems improbable that this explanation can be applied to sexual imprinting: the remarkably strong and stable effects of three short choice tests point to causes different from effects of mere exposure. The findings suggest that the stability of filial and of sexual imprinting cannot be explained by the same causes. This does not imply that Bateson's model is not useful to understand the results. However, factors contained in the sexual context of exposure appear to be necessary to explain the drastic effects that were found.

Finally, we should remember that the results need not necessarily reflect development occurring under natural conditions. Consolidation of preferences developed under influence of early experience may occur much earlier in development if contact with the rearing species is not prevented during the stage that sexual behaviour develops in males. The findings reported here may be due to retardation of this process as a result of separation of the males from the rearing species during this stage.

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EARLY EXPERIENCE AND SONG LEARNING IN ZEBRA FINCHES *TAENIOPYGIA GUTTATA*

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ABSTRACT. Young male Zebra Finches exposed to a series of song tutors learn their songs after independence from their parents. However, experience before that time has important influences on tutor choice. Given a choice young males tend to select a tutor who looks and sounds like the father. Sexual imprinting may thus bias song learning, but the two are not inextricably linked, as birds exposed to two colour morphs may imprint on one and learn song from the other.

Keywords: Zebra Finch, *Taeniopygia*, song, learning, imprinting.

INTRODUCTION

Learning plays a role in the song development of all the species of songbirds (Oscines) that have been studied so far (see the survey by Kroodsma & Baylis 1982). Yet, within this broad pattern, there are many variations. The timing of song learning is one feature in which species differ markedly. At one extreme, young birds may learn entirely as juveniles before they start to sing themselves (e.g. Song Sparrow *Melospiza melodia*, Marler & Peters 1987), while at the other learning may take place throughout life (e.g. probably the Canary *Serinus canarius*, Nottebohm & Nottebohm 1978).

These differences between species are particularly striking as they can be found, as in the two species mentioned above, between quite close relatives. However, most species that have been studied appear to be "age limited" learners, with sensitivity to song learning restricted to a particular period, often early in life, in a way very similar to the phenomenon of imprinting, so that analogous questions can be asked about the two processes. As with imprinting (see Kruijt this symposium), it is becoming clear in studies of song development that the sensitive phase is far from being a fixed phenomenon which starts and finishes automatically according to some physiological clock, but is adjusted in time by many aspects of experience. This is nowhere more obvious than in studies of the Zebra Finch (Slater et al. 1988).

In many ways this species is ideal for laboratory studies of this sort, as originally appreciated by Immelmann (1969) in his pioneering work. It is easily kept and bred in captivity, it breeds throughout the year, and it has a generation time of around three months so that one does not have to wait too long before young males mature and start to sing. Only males sing and the song is a short, simple phrase used both in courtship and by solitary males. While the definition of song elements and comparison between songs is not as simple as in many other species, reasonable consistency between observers has been found with the use of sound spectrograms.

THE BASIC PATTERN OF SONG LEARNING

If young male Zebra Finches are left with their parents until 35 days, at roughly the time they would normally become independent in the wild, and then moved into the company of another singing male, the song that they sing is based on that of the latter rather than on the father's (Eales 1985). However, if left with the father till 65 days old, they will copy his song rather than that of a male they encounter thereafter. Thus, in these laboratory conditions, song learning appears to take place between 35 and 65 days of age.

What happens if young males do not encounter a suitable tutor during this period? Various lines of evidence suggest that they may, depending on the exact conditions, produce sounds heard before 35 days or be prepared to learn new sounds encountered after 65 days. The latter may occur, for example, when earlier experience has been inadequate for song memorisation. Eales (1987) found young males raised by females alone to develop songs consisting of a succession of female call notes. If the father was then reintroduced at various stages, even after 65 days, his song would be memorised. However, in the context of the current symposium, the most interesting effects are those of experiences before 35 days. Sexual imprinting in Zebra Finches is thought to occur primarily at this stage (Immelmann 1985), and our results therefore suggest that it precedes song learning, but the two processes may still be linked. Sexual imprinting might, for example, bias young birds towards choosing tutors of one particular type rather than another. Our recent experiments with colour morphs (Mann et al. in press) suggest that this is the case.

PARENTAL MORPH AND SONG LEARNING

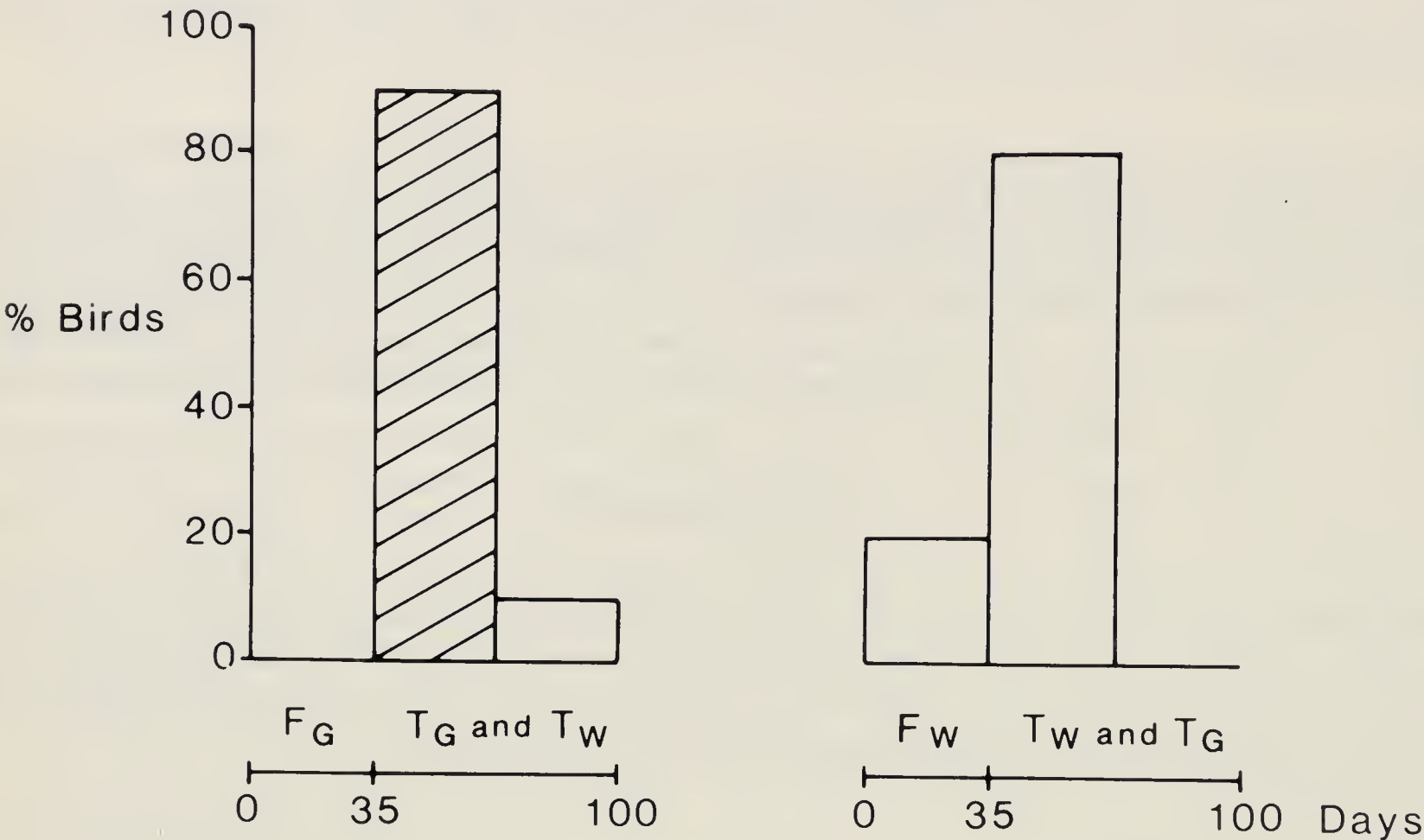
In addition to the wild-type or grey form, captive Zebra Finches have been bred to produce various different morphs. In our experiments we have used young birds reared either by grey parents or by ones of the chestnut-flanked white morph. Adults of this morph are white rather than grey, but retain the sexually dimorphic plumage characteristics of the wild type. By cross-fostering we have obtained young birds reared by adults of their own morph or of the other one, either in broods of a single morph or in mixed broods.

We have not so far found any differences in results according to the morph of the young birds or of their siblings. However, the parental morph has a marked impact on song tutor choice. Where a single adult male tutor is presented between 35 and 65 days, as mentioned above, young birds will normally learn the song of that individual. But if it is of a different morph from that of the parents, this pattern becomes disrupted, with elements from the father's song being reproduced more often, and with learning also occurring from a tutor of the father's morph first encountered after 65 days.

The influence of parental morph is even more strikingly illustrated when young males are given a choice of two tutors, one of each morph, between 35 and 65 days. This experiment involved 10 males with grey parents and 12 with white ones. In only one out of the 22 young birds were more elements learnt from the tutor whose morph contrasted with that of the parents (Figure 1).

These results point to parental appearance having a strong directing influence as far as tutor choice is concerned. Is it simply that sexual imprinting, completed before 35 days, determines tutor choice? Our results on mate choice suggest that this may not be the case. All the young males in these experiments were given tests in which they were placed in the central section of a triple cage with females of the two different

A. SONG TUTOR PREFERENCE



B. MATE PREFERENCE

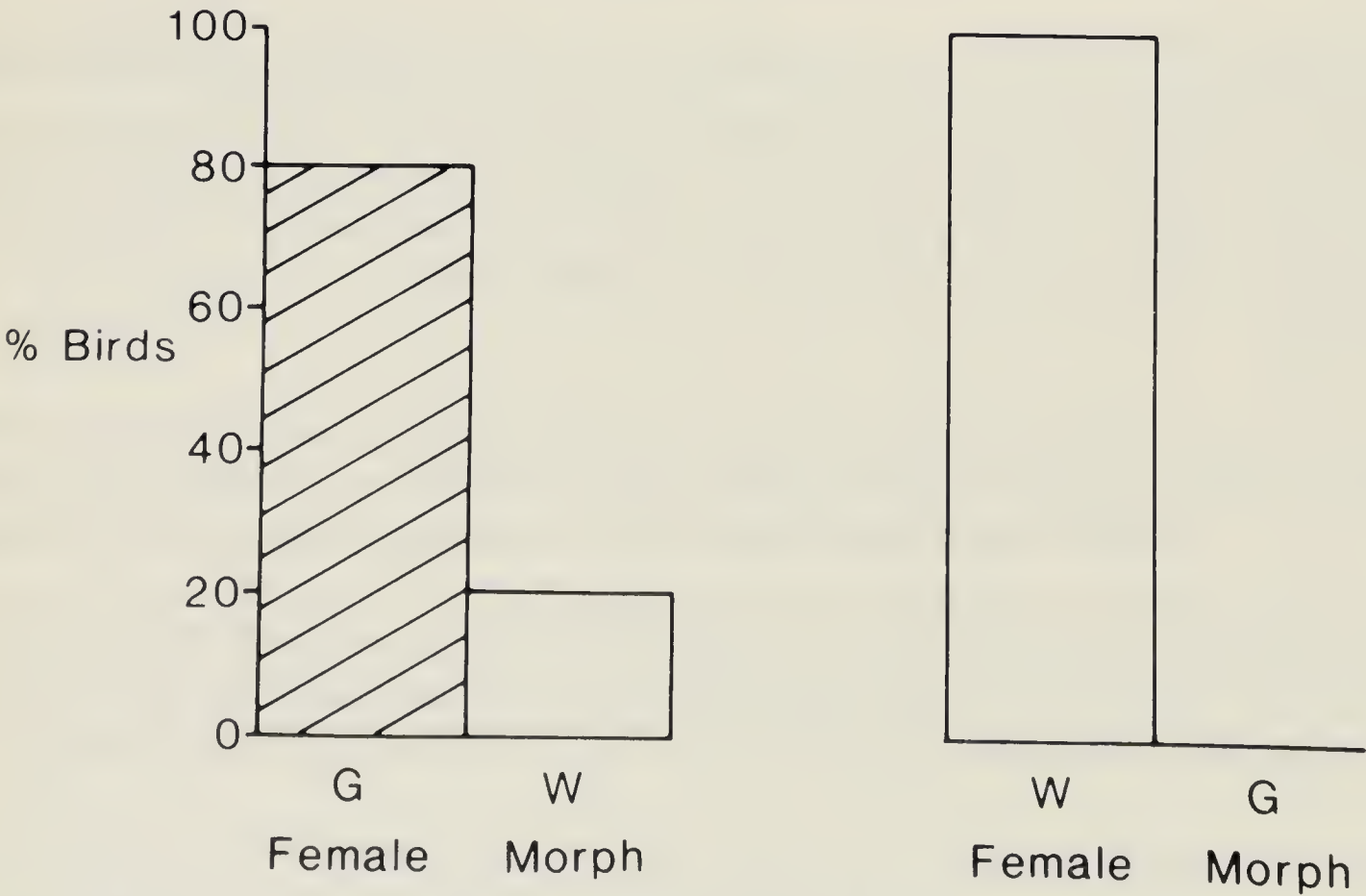


FIGURE 1 – The song tutor preference (A) and mate preference (B) of young birds exposed to both grey and white male tutors from 35-100 days. N=10 in all histograms, some birds not having made clear choices. Open column, white preferred; hatched column, grey preferred. F_G , father grey; F_W , father white; T_G , tutor grey; T_W , tutor white (from Mann et al. in press).

morphs in the end compartments. Both females had been reared by pairs of the male's morph to equalise their responsiveness to him as much as possible. His preference was assessed by the number of songs he directed to each female.

In most of these experiments the male showed a preference for a female of the same morph as that of his parents, this being also that of the tutor he had learnt from. However, this is hardly surprising on the simple grounds that the young bird had had more experience of that morph than of the other one. It is more interesting that there were some birds which showed the opposite result: they had clearly learnt their song from the tutor of one morph but preferred to court a female of the other (Table 1). The two processes thus appear to be to some degree dissociated. This result is in line with the findings of Clayton (1988). She found that young males raised by pairs in which one partner was a Zebra Finch and the other a Bengalese would often choose a song tutor of one species and a mate of the other.

TABLE 1 – The mate choice and song tutor choice of 47 Zebra Finch males combined from various experiments in which they were exposed to two morphs (data from Mann et al. in press)

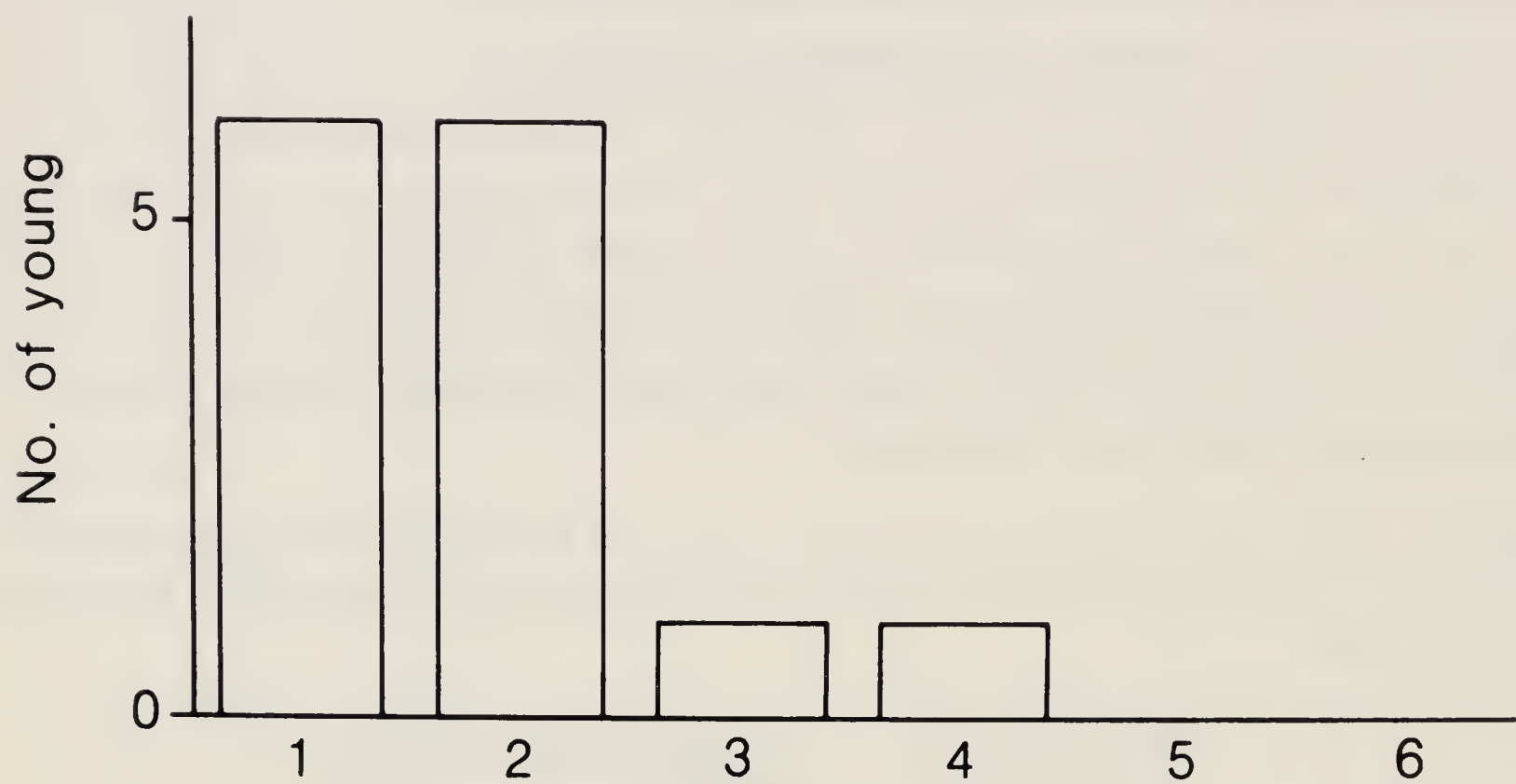
Morph chosen as song tutor	Morph chosen as mate	
	Parental	Other
Parental	30	8
Other	2	7

Despite these findings, it is possible that the effect of colour morph on both sexual preference and tutor preference results from the same imprinting process. Cases where the choices differ might, for example, arise where the song tutor of the appropriate morph seldom sang, or where one of the females was much more responsive than the other in the mate choice tests. In other words strong behavioural differences between the two individuals in choice tests are likely to override the effects of imprinting on colour morph. This may have been particularly important in the mate choice tests as there the preferred mate colour was less often that of the parents than was the preferred tutor colour (Table 1). Another possibility which might account for this is if mate preference is more susceptible to modification by subsequent experience (for example, by exclusive exposure to a novel morph from 35 days onwards) than is song tutor preference. The results of Kruijt (this symposium) certainly point to mate preference being considerably more flexible into adulthood than originally supposed. Again, such a difference from song might occur even though the initial preferences developed from the same imprinting process.

THE PROGRESSIVE CHANNELLING OF PREFERENCE

Despite a great deal of work in the past few years, we still cannot be sure from whom young Zebra Finches learn their songs. Independence does not occur abruptly at 35 days, nor does the sensitive phase for song learning switch on in a step-like fashion at that age. As with many other species, social factors are important for song learning. As well as choosing a tutor that looks and sounds like their father, young Zebra Finches also tend to learn from an individual that is aggressive towards them (Clayton 1987). This might also lead them to learn from the father if he becomes more aggressive to them at around the time of independence, but we do not yet know.

8 Tutors simultaneously



7 Tutors in sequence

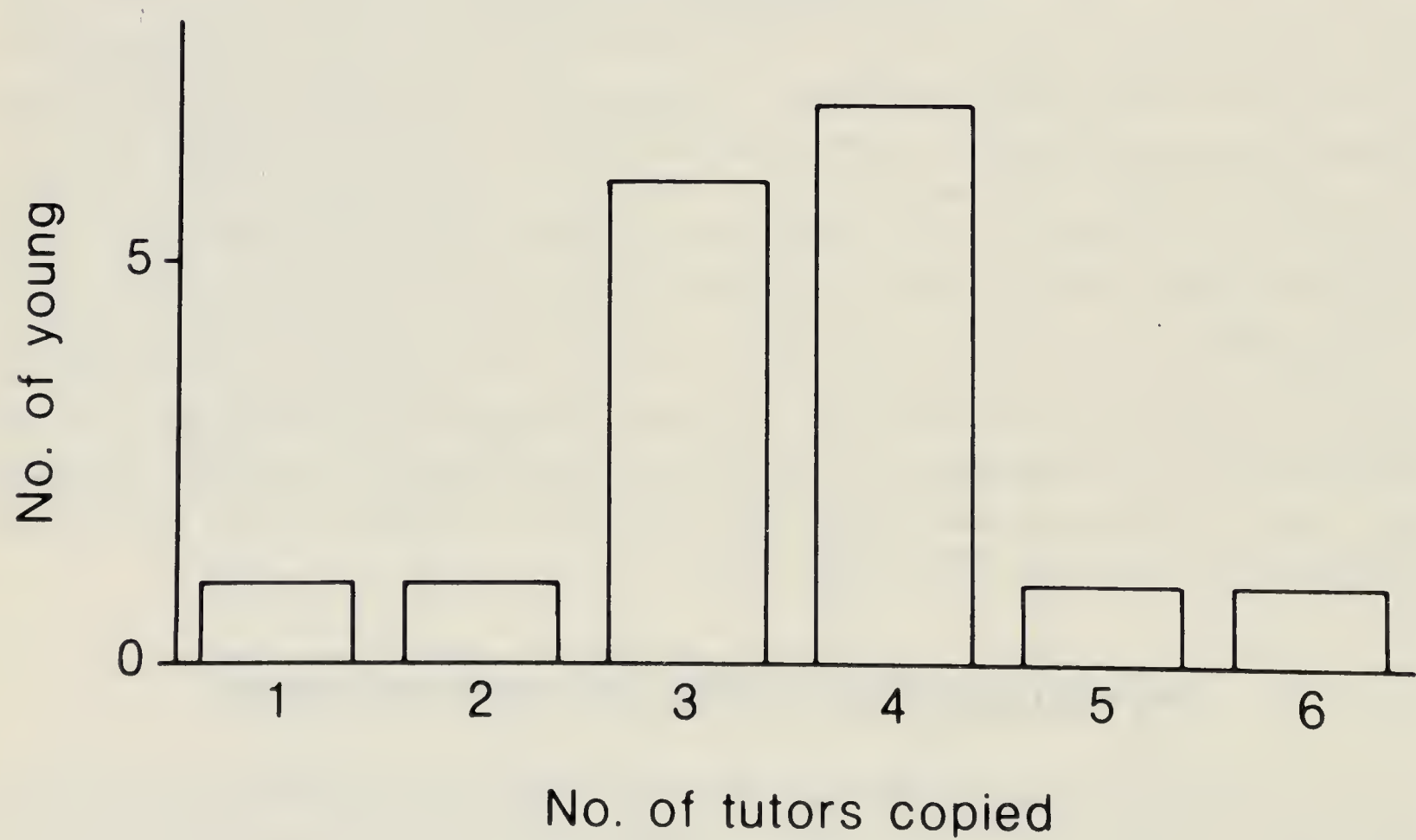


FIGURE 2 – The number of different tutors whose songs were copied by young birds in two different situations. Top: Eight tutors simultaneously, including the father, the birds being hatched and reared in an aviary. Bottom: Seven tutors in a row, the father until 35 days and then six other males for 5 days each until day 65.

What does appear certain is that experience leads to a progressive narrowing of preferences. Experience with the parents before independence channels preference, both for mates and for song tutors, towards individuals with similar characteristics thereafter. If such individuals are not present the process of song learning is delayed or disrupted. The same process of channelling is probably responsible for the fact that young birds tend to latch on to particular tutors. When more than one tutor is present simultaneously, the young birds most often learn complete songs from one of them rather than combining elements from several. Thus, in aviary experiments, when eight adult males were present throughout the sensitive phase, we have found that few young birds learn from more than two adults (Figure 2). On the other hand, when young males are exposed to a succession of six tutors, for five days each between day 35 and day 65, most of the songs they develop include elements from several of the tutors (Kolmogorov-Smirnov two sample test, Chi-square = 16.8, $P < .001$). In this situation the young bird does not have the opportunity to associate with one or two tutors to the exclusion of others, but is forced into spending equal time with each of them. However, it is interesting that not all the tutors are as likely to be copied. A disproportionate number of elements are incorporated from the two experienced between 55 and 65 days: of 112 elements copied by 17 young birds from the six tutors, 55 were from these two (Kolmogorov-Smirnov one sample test, $P < .01$). This suggests that later experience may overwrite or modify that obtained earlier.

As with imprinting, a further social influence on developing preferences may be that of siblings (see Dyer this symposium), though we have not studied it yet in detail. What is clear is that young males given adequate tutoring in groups often develop songs that are quite different from each other. However, siblings can certainly affect each other: for example, the songs of the males in groups not exposed to song tutors do tend to be similar (unpublished observations). While our results also suggest that social contact between young birds and adults leads them to produce similar songs, young birds often develop songs differing from those of their tutors. The possibility that they may benefit from having songs that are slightly different (see ten Cate this symposium) remains to be explored.

SIMILARITIES AND DIFFERENCES IN MECHANISM

As well as asking whether sexual imprinting affects song tutor choice, we can examine the fundamental mechanisms involved in each and ask whether they have similarities (ten Cate, 1989). One concept that does seem potentially useful in both cases, is that of "updating" (Bateson pers. comm., Ryan & Lea 1990). Although this idea has been developed in relation to imprinting, many of our results on song learning can be explained in similar terms. Thus a bird which has experienced one song and is then exposed to a slightly different one may latch on to the latter and learn it by modifying its earlier memory, while it would be much less likely to memorise songs very different from those it had experienced, or store them as separate representations. Thus a Zebra Finch reared by Bengalese Finches may be less prone to learn Zebra Finch song after independence because it differs markedly from that of its foster father.

There are, however, also fundamental differences between imprinting and song learning. While imprinting is a process of memorisation, song learning involves production as well. A period of practice is necessary to perfect the song even after its details have been memorised. Our evidence suggests that companions may have an

important role here, but one which is distinct from that of providing models to be copied. A Zebra Finch may fail to learn the song of an inadequate tutor, such as a Bengalese Finch, but the social stimulus may lead the young bird to practise and so crystallise a song based on elements heard earlier. If a bird lacks a tutor at this stage it may delay learning until later, but an inadequate tutor may encourage it to practise so that it develops a song based on sounds heard earlier.

CONCLUSION

Our experiments show that a great many factors can alter the timing of song learning in Zebra Finches. Birds which have inadequate experience during the sensitive phase may alter their songs later, or may recall and use sounds heard at an earlier stage. It appears that experience progressively channels the preferences of the young birds so that they become less prepared to accept tutors who differ visually or vocally from those they experienced earlier. The acceptance of a tutor also depends on the particular social experience the young bird has with that tutor. While many of the factors affecting song tutor choice are similar to those involved in sexual imprinting, the fact that the two processes can be dissociated argues against incautious generalisation between them.

ACKNOWLEDGEMENTS

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SEXUAL IMPRINTING, MATE PREFERENCES AND PLUMAGE EVOLUTION

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ABSTRACT. Sexual imprinting has been suggested to promote rapid speciation and also to have a stabilising effect on the evolution of plumage characteristics. This view about the evolutionary significance of imprinting is based on the assumption that imprinting results in a preference for those individuals which are most similar to the imprinting stimulus. This assumption may seem true if the preference for the familiar stimulus is compared with that for a different species or colour morph, but it seems not to hold when preferences are examined in more detail. Experimental evidence suggests that specific, slightly deviant, versions of the imprinting stimulus may be preferred over the original one. The 'directionality' in the preference suggests that imprinting may play a role in driving plumage evolution in specific directions. This contrasts with the traditional views of the evolutionary significance of sexual imprinting, but seems more consistent with the presence of imprinting in closely related, sympatrically occurring groups of birds.

Keywords: Imprinting, mate choice, plumage, evolution, speciation, sexual selection, Japanese Quail, Zebra Finch.

INTRODUCTION

Early experience may have a profound influence on mate preferences. Many birds prefer mates with morphological characteristics similar to the rearing species, even when this is not their own. This phenomenon of 'sexual imprinting' is known from many species of ducks, geese, gallinaceous birds, parrots, doves, songbirds and others (e.g. Immelmann 1972).

Sexual imprinting is usually considered to be demonstrated when birds prefer individuals of the rearing species or colour morph over other species or morphs. Lorenz (1935) originally suggested that imprinting led to a preference for characteristics of the species rather than one for objects which matched the parents precisely. Nevertheless, the finding of a preference for the rearing type has been interpreted as a preference for "those objects that bear the closest similarity to the object the individual had originally been exposed to" (Immelmann 1975). As has been noticed by Bateson (1982), it is this axiomatic view of the outcome of the imprinting process that underlies models aimed at assessing the evolutionary consequences of sexual imprinting.

Below, I shall first outline the traditional views on the evolutionary consequences of imprinting. Next I shall argue that, at least in some species in which mate preferences are thought to arise primarily as a consequence of sexual imprinting, the most preferred mates are *not* those most similar to the rearing type, but rather those differing from it in a specific way. This finding serves as a basis for a re-examination of the potential evolutionary consequences of sexual imprinting.

SEXUAL IMPRINTING AND EVOLUTION: THE TRADITIONAL VIEW

It has been long recognised that differences in mate preferences arising from differences in early experience may have evolutionary consequences. For instance, the maintenance of a segregation between the white and blue colour phases of the Snow Goose *Anser caerulescens* is considered, at least partly, to be a consequence of selective mating based on sexual imprinting (Cooke 1988). Indeed, various simulation models have indicated that the presence of a mate preference based on sexual imprinting in a population consisting of different colour morphs may lead to non-interbreeding groups or to a stable equilibrium between in- and outbreeding, depending on the precise circumstances (O'Donald 1960, Mainardi et al. 1965, Kalmus & Maynard Smith 1966, Seiger 1967, Seiger & Dixon 1970, Scudo 1976). For this reason sexual imprinting has been suggested as likely to promote rapid speciation (Immelmann 1975, Kalmus & Maynard Smith 1966, Seiger 1967). At the same time, a strong detailed preference for the rearing type will have a stabilising effect on plumage characteristics, and birds with a deviant plumage will be less likely to be acceptable as a mate. As phrased by Seiger (1967): "imprinting would tend to limit the number and types of forms in a dimorphic population to those which already exist in the population. If a new colour mutant occurred, or if an individual of a new colour migrated into the population, individuals bearing the new colour would be rejected by the rest of the population." It should be noted that this situation creates a paradox: if birds differing from the rearing type are not acceptable (or less preferred) as mates, how may different morphs evolve, or how can a further evolution of given plumage variants occur?

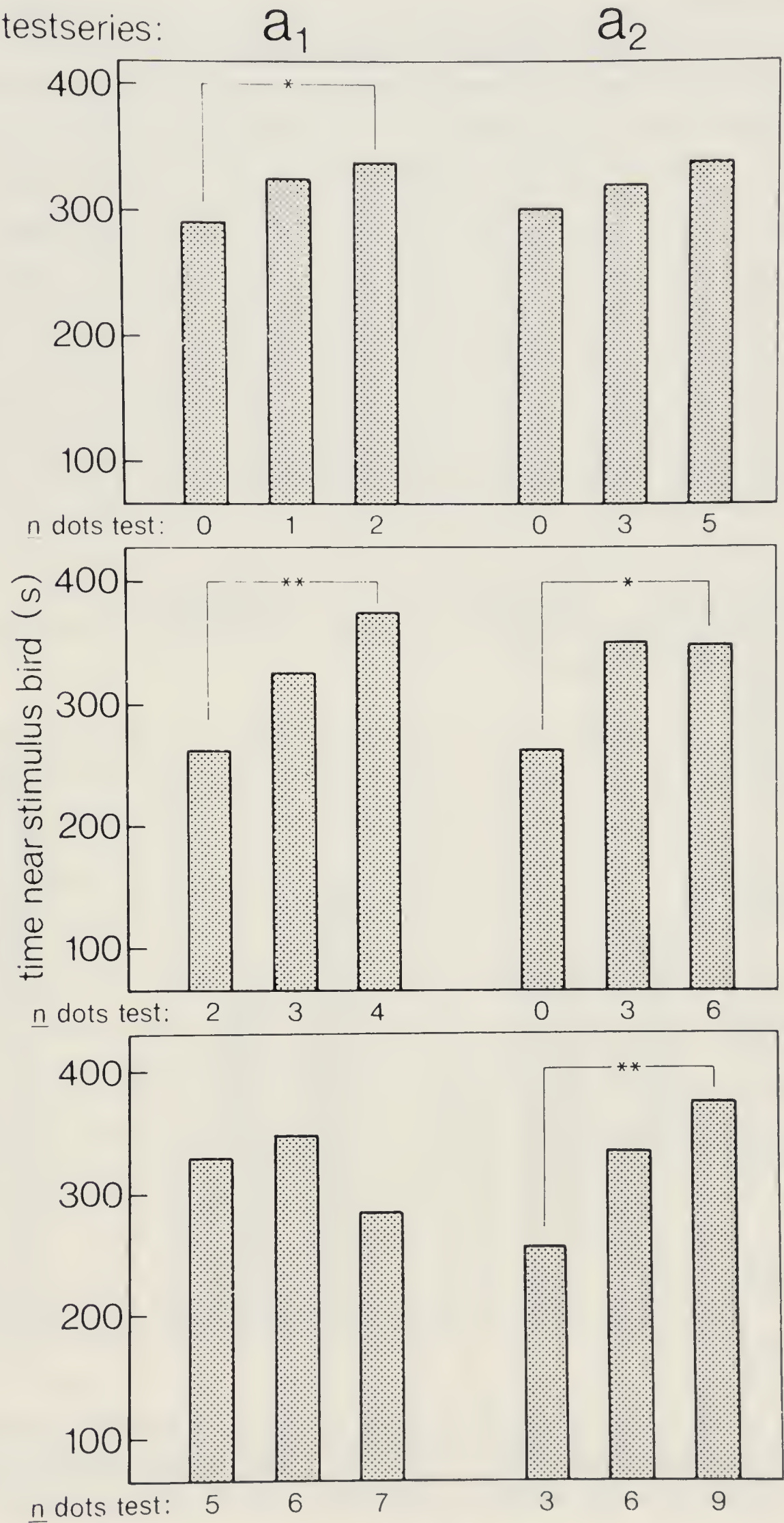
Within the above system, the only possible way for a new morph to get established would be if birds prefer mates strongly resembling their siblings rather than their parents. Then a new plumage mutant may, by being preferred by its siblings, be able to establish itself. However, there is evidence that, at least for some species, parental influence on sexual imprinting is stronger than sibling influence (Kruijt et al. 1983). So, if one accepts that sexual imprinting results in a strong and precise mate preference based on parental plumage, one can argue that it will hamper plumage evolution for the same reason that it will rapidly lead to non-interbreeding groups once more morphs are present; the stronger and more precise the preference resulting from sexual imprinting is, the stronger its effect on speciation will be once several morphs are present. On the other hand, the stronger and more precise the preference is, the less likely it is that any mutant plumage will get a chance to establish itself as a new morph, nor will a further evolution in plumage characteristics occur. Whereas the first phenomenon has been held responsible for the observation that sexual imprinting seems particularly common in closely related bird species, assumed to have evolved rapidly (Immelmann 1975), the second phenomenon seems at odds with this observation. A way out of this paradox is suggested by recent research addressing the question of whether the preference resulting from imprinting is indeed one leading to a preference for those individuals which resemble the rearing type most closely.

IMPRINTING AND MATE PREFERENCES

In a number of experiments it has been found that birds may prefer mates which differ from the rearing type in their appearance. This does not necessarily imply that they



exposure
to 0 dots



prefer the plumage characteristics of such mates over the familiar plumage. Pair formation and mating is usually the end of an interactive process in which both sexes play a role and in which potential partners may not only respond to appearance but also to each other's visual displays or vocalisations. A vigorously displaying mate, for example, with a less familiar plumage may be preferred over a less vigorous but more familiar one (ten Cate 1985, 1988). Nevertheless, when such factors are controlled for, there is evidence to suggest that some birds may still prefer mates which deviate in appearance from the rearing type. This preference does not show up when birds are given the choice between the rearing morphs or species and one looking quite different, but it may when the choice is offered between a stimulus bird of the familiar type and a slightly deviating one. One example of this is provided by the Japanese Quail *Coturnix coturnix japonica*. Bateson (1978) showed that male Japanese Quail reared with wild type individuals preferred wild type, brown, females over white ones. However, unfamiliar brown females were preferred over familiar ones

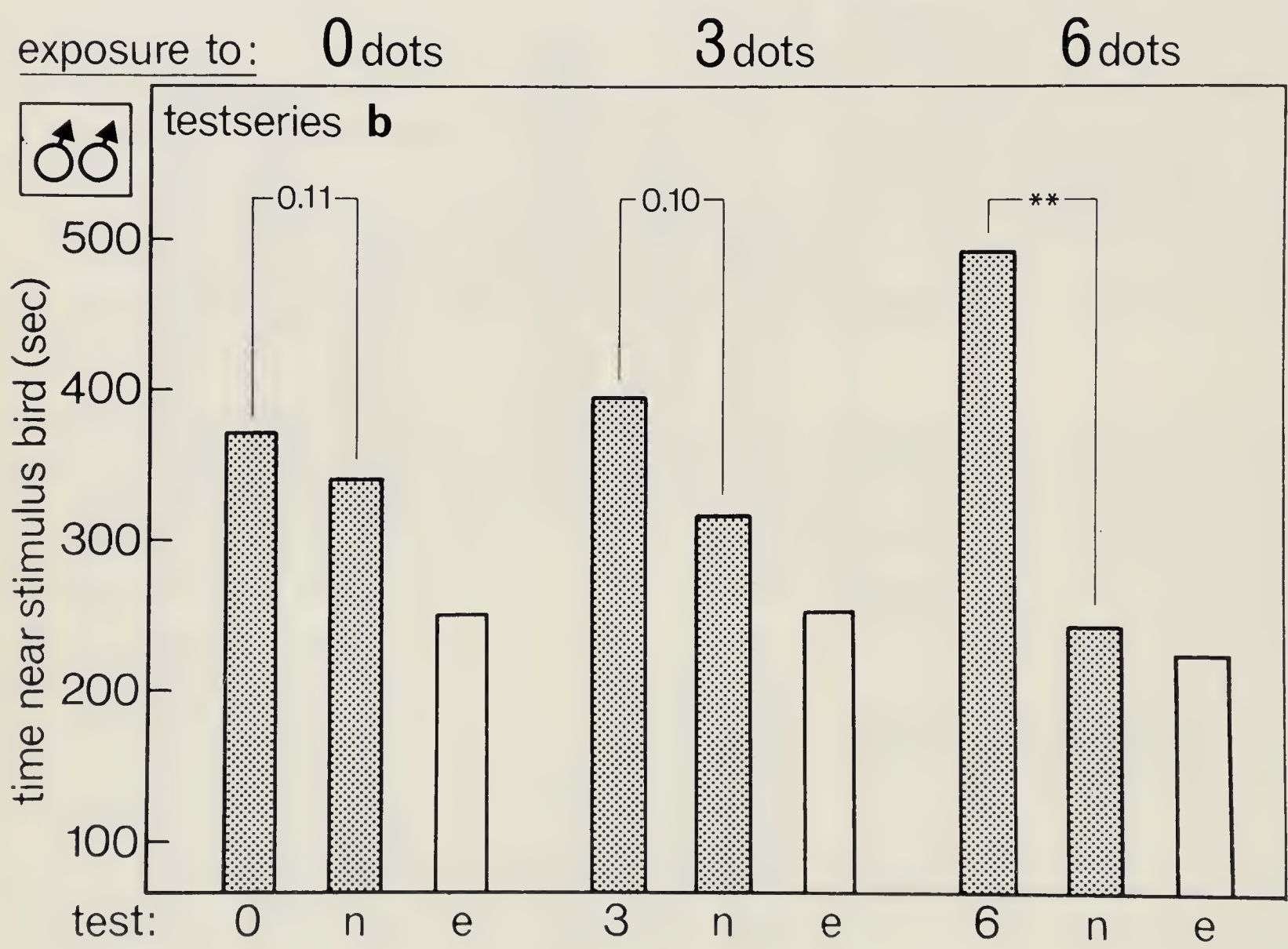


FIGURE 2 - Time spent near a stimulus bird with the familiar number of dots (0, 3 or 6, depending on rearing condition), near a bird with the wild type plumage (n), and near an empty stimulus compartment (e). See Figure 1 for testing procedure.

Further experiments (Bateson 1980, 1982) showed that both males and females preferred those brown partners that were slightly different from the birds used as imprinting stimuli. When reared with siblings, for instance, and offered a choice between unknown siblings, first cousins, third cousins and unrelated quail, both males and females preferred first cousins. Later experiments confirmed this finding and, in addition, suggested that the degree of phenotypic variability within family and population was important for which relatives were preferred (Bateson 1988).

The findings may suggest that any slight deviation away from the familiar type may make a novel bird more attractive, but does it? This was examined in an experiment in which Japanese Quail chicks were exposed to one of three different types of imprinting stimuli. These were adult white quail with either zero, three or six black dots dyed on their breast feathers (see ten Cate & Bateson (1989) for a detailed account of this experiment). When adult, preference tests were carried out in which each bird was given a choice between one individual with the familiar number of dots and two with either more or fewer dots. In one series of tests (a1, see Figure 1) the difference between the familiar number of dots and the novel ones was small, in another series (a2) the difference was larger. The results (Figure 1) demonstrated that, on the whole, male quail had a significant preference for those stimulus birds with the highest number of dots over those with the lowest number of dots; in particular they seem to dislike mates with fewer dots than the familiar stimulus. When males were given the 'classic' imprinting test: the choice between a white bird with the familiar number of dots and a bird with the normal, brown, wild type plumage, the familiar bird was preferred (Figure 2). So, the preference for a dotted bird is not due to some dominating naive preference for the wild type plumage. A preference which is demonstrably affected by early experience may thus, at the same time, show a bias towards specific deviations.

Similar findings exist for the Zebra Finch *Taeniopygia guttata*. Due to the inspiring and pioneering studies of Immelmann, this species has become a classic example of a bird in which mate preferences in both sexes are affected by early experience (Immelmann 1969, Kruijt et al. 1983, ten Cate & Mug 1984, ten Cate 1989). Nevertheless here also the most preferred mates seem to be individuals slightly deviant from the familiar. Immelmann (1959) showed that an artificial decrease in plumage contrast made males less attractive as a mate, but when contrast was artificially increased by painting white dots on the normally plain brown cheeks, these males were preferred over normal males. More recently, Burley and co-workers demonstrated that various changes in the appearance of both sexes, like in bill colour or the addition of colour bands (Burley et al. 1982, Burley 1985a, b, 1986, Burley & Coopersmith 1987) led to preferences which were asymmetrical around the wild type appearance. It will be clear that the above experiments leave unanswered questions like whether the preference for more dots is open ended or whether it depends upon the number of dots in the familiar bird. Further research will be necessary to address such questions and to examine the underlying mechanism(s). At present, one hypothesis is that a combination of imprinting and subsequent habituation result in an internal representation that differs slightly from the imprinting stimulus. Alternatively, two separate mechanisms may be involved; one being imprinting, leading to a precise storage of information, and the other being a developmentally independent perceptual mechanism, giving rise to a preference for specific characteristics in potential mates; in combination these mechanisms may lead to a preference biased towards specific novel mates.

To conclude, species in which mate preferences are primarily determined by early experience do, at the same time, provide evidence that the most preferred mate is one which differs in a specific way from the familiar stimulus bird. The phenomenon may be more widespread than is known at present, as in most cases choice tests using two different morphs or species will not have been sensitive enough to detect preferences of this type. Assuming that more detailed experiments will indeed reveal the

phenomenon in other groups of birds, we may now return to the question of how this finding alters the view about the evolutionary significance of sexual imprinting.

IMPRINTING AND PLUMAGE EVOLUTION RECONSIDERED

Japanese Quail and Zebra Finches may have preferences for mates which differ from the imprinting stimulus, but at the same time the preferred difference from the familiar seems so small that both will mate assortatively when given the choice between two morphs of their own species. For the Zebra Finch this was demonstrated first by Immelmann et al. (1978), in an experiment involving white and wild type birds. More recently Clayton (1990) showed that two subspecies of the Zebra Finch ('Australian mainland' *Taeniopygia guttata castanotis* and 'Timor' *Taeniopygia guttata guttata*) mated assortatively. Her findings indicated that the assortative mating was, at least to some extent, influenced by plumage characteristics of these subspecies. This shows that even when the appearance of the most preferred mate is not identical to that of the stimulus encountered early on, sexual imprinting may still promote segregation of various morphs in a mixed population, as predicted by various models for the evolutionary consequences of sexual imprinting (Kalmus & Maynard Smith 1966, Seiger 1967). However, a consequence of the preference for specific novel mates is that the behaviour towards new plumage mutants may be quite different from that expected traditionally. Whereas earlier views, such as those quoted from Seiger (1967) in the introduction, predicted a strong selection against deviant birds, the above findings suggest that certain deviant birds may instead gain selective advantage over normal birds. Thus, specific mutations might be able to get rapidly established in the population, like, for instance, black dots in a population of white quail. In addition it must be noted that the offspring of such mutants will not only be likely to inherit the mutations, but, due to experience with the mutant appearance, will also have a preference for an even more exaggerated version of it. So, preference may evolve together with actual appearance. Although the evolutionary significance of this effect may need more sophisticated mathematical modelling, the intuitive notion is that such a mechanism will drive rather than hamper plumage evolution. If so, the occurrence of imprinting in rapidly evolved or evolving groups of birds becomes a likely instead of an unlikely finding and may even serve as a pre-adaptation for plumage evolution to occur.

DISCUSSION

Abandoning the axiomatic view that sexual imprinting goes together with a precise preference for the rearing type leads, as outlined above, to a more consistent view of the role of imprinting in speciation and plumage evolution. It does, of course, raise new questions too. Not only questions about the causal mechanisms underlying the preference for deviant birds, but also questions for the functional significance of such a preference. Why should birds like to mate with specific deviant birds rather than with those of a familiar type? Several, not necessarily mutually exclusive, hypotheses can be put forward about the functional significance. First, as suggested by Bateson (1978, 1980), preferences for slightly deviant birds may be a way to obtain an optimal balance between in- and outbreeding. It will, on the one hand, prevent birds from mating with close relatives and, on the other, prevent them from mating with birds

which are too dissimilar and which might belong to a different ecologically adapted population. Following this line of reasoning, one should not attach too much significance to the finding that *specific* deviating birds are more attractive than others, as it might be an epiphenomenon of the mechanism producing the shift away from the familiar type. Another hypothesis might be that specific deviations away from the parental plumage indicate mates of better quality. In this line of thought the preferred plumage modifications are those which can only be afforded by birds with superior physical or genetic qualities. This hypothesis links sexual imprinting to the process of sexual selection (ten Cate & Bateson 1988). A third hypothesis has a connection to the presence of imprinting in rapidly evolving groups. According to this hypothesis birds of a species which lives sympatrically with a closely related species would do best to prefer mates which least resemble the related species, so as to avoid deleterious hybridization (Burley 1986). To discuss the plausibility of these hypotheses is outside the scope of this paper. However, it will be clear that birds may benefit from choosing slightly deviant mates, providing functional explanations for the existence of such preferences.

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SYMPOSIUM 17

NOCTURNALITY IN BIRDS

Conveners G. R. MARTIN and M. de L. BROOKE

SYMPOSIUM 17

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INTRODUCTORY REMARKS: NOCTURNALITY IN BIRDS

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ABSTRACT. A strictly nocturnal life style among birds is rare, probably involving less than 3% of all species. It is found primarily among species from three orders (Strigiformes, Caprimulgiformes, Apterygiformes). Occasional nocturnal behaviour is more common and involves species from many orders. Among such nocturnal behaviours are migration, foraging, singing (mate attraction) and visiting colonies. In order to investigate the sensory problems of nocturnal behaviour it is necessary to appreciate the wide range of light levels which occur naturally at night and the manner in which night length varies with latitude and season. Knowing what birds do at night and why and how they do it has important implications for a thorough understanding of the ecology and conservation of many species.

Keywords: Nocturnal, senses, vision, foraging, migration.

INTRODUCTION

While the majority of birds roost throughout every night of their life, a significant proportion of species are regularly active at this time. Some species may be strictly nocturnal, rarely conducting any significant activities by day, while others may conduct just specific activities at night, often at only particular times of the year. Knowing what these birds do at night, and why and how they might do it, raises many questions essential for understanding aspects of the behaviour and ecology of birds. By investigating the sensory problems of nocturnal behaviour it is possible to understand something of how an animal gains information from, and uses this to interact with, its environment.

The papers in this symposium do not attempt a comprehensive review of nocturnal behaviour in birds. They highlight particular aspects of nocturnal behaviour which we believe raise a number of important questions concerning sensory capacities, ecology and conservation. They deal with behaviours which are specifically nocturnal, that is, those which may occur throughout the night, as opposed to crepuscular activities, which occur principally in the twilight periods.

STRICT NOCTURNALITY

A strictly nocturnal life style (in which all activities of the annual life cycle are completed between sunset and sunrise) is rare among birds. Strictly nocturnal birds come principally from three orders; Strigiformes (owls), Caprimulgiformes (Oilbird, nightjars, potoos, owlet-nightjars and frogmouths) and Apterygiformes (kiwis), which together contain less than 3% of all bird species. Establishing strict nocturnality is particularly problematic and for many species the habit is inferred from taxonomic relationships and scattered field observations rather than from systematic study. Certainly not all species in these orders are strictly nocturnal and among the owls probably less than half the species fall into this category. Beyond these three orders a strictly nocturnal

life style is probably found among just a few species of shorebirds (Charadriiformes) and three species of near flightless parrots (Psittaciformes: Ground Parrot *Pezoporus wallicus*, Night Parrot *Geopsittacus occidentalis* and Kakapo *Strigops habroptilus*). At one time the Kagu *Rhynochetos jubatus* (Gruiformes) was regarded as strictly nocturnal but recent study shows that the bird only becomes nocturnal during incubation (Neyrolles & Naurois 1985). This example highlights the uncertainty of knowledge about the nocturnal behaviour of many species.

The rarity of strict nocturnality among birds is probably principally due to the inadequacy of vision as a means of guiding foraging and flight, especially in spatially complex habitats such as woodlands, at low natural light levels (Martin 1990a). These sensory limitations have two consequences for nocturnal behaviour; (1) They restrict the types of prey and foraging techniques which can be exploited by nocturnal feeders (see Martin, this symposium), and (2) to be mobile in complex conditions necessitates a highly sedentary lifestyle. In open habitats the limitations upon visual performance under natural night time conditions are less severe and probably do not demand a sedentary habit (Martin 1990a).

OCCASIONAL NOCTURNALITY

In addition to the relatively few habitually nocturnal birds there are many which, although usually regarded as diurnal in their habits, may on occasion be active at night. The most important examples of such occasional nocturnal behaviours are as follows.

Migration

Populations and individuals in a wide range of passerine and non-passerine species may migrate along sections of their migratory route at night. However, it seems few, if any, species are obligate night migrants (see Kerlinger & Moore 1989, Martin 1990a,b, Moore & Kerlinger this volume, for reviews of aspects of nocturnal migration).

Singing, calling and aerial displays

In a number of otherwise diurnally active passerine and non-passerine species, males may sing or call throughout the night. In some passerines (such as *Acrocephalus* warblers and the Nightingale *Luscinia megarhynchos*) this behaviour is exclusively concerned with mate attraction (Cramp 1988, pp. 621 and 632). Some male shorebirds which give aerial displays at dusk may sometimes extend this behaviour into the night. (See McNeil in this symposium.)

Attendance at colonies

Many procellariiform and some charadriiform seabirds enter and leave nest colonies exclusively at night. This is primarily to avoid the attacks of diurnal predators. Particularly well studied examples include Manx Shearwaters *Puffinus puffinus* (Brooke 1990) and Swallow-tailed Gulls (Harris 1970).

Foraging

Many species of pelagic seabirds (Procellariiformes), shorebirds (Charadriiformes), waterfowl (Anseriformes) and herons (Ciconiiformes) have been recorded foraging by both night and day. In these birds foraging is not necessarily exclusively nocturnal;

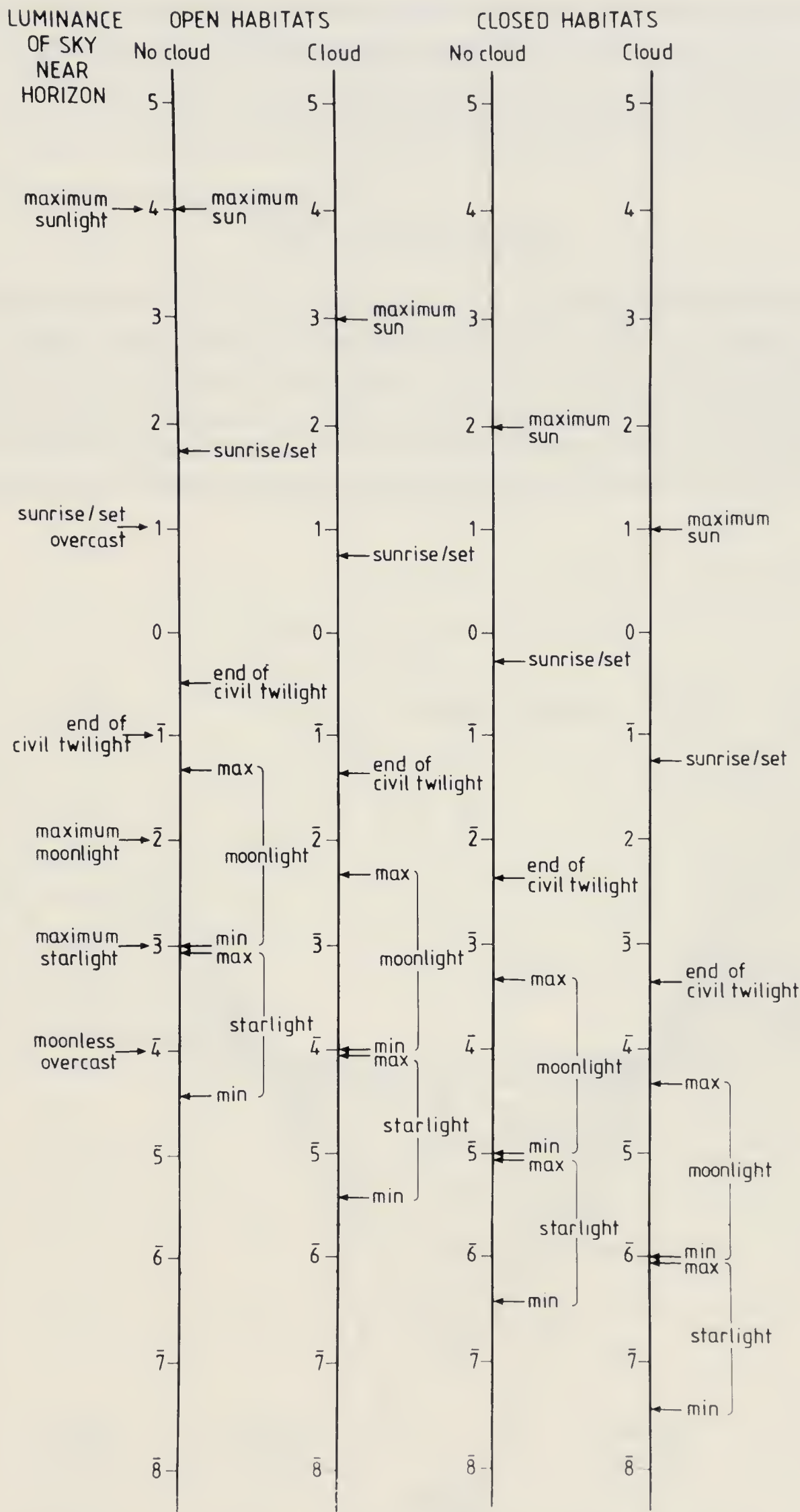


FIGURE 1 - The luminance (log cd/metre) of a natural substrate, such as leaf litter or grass, when illuminated by various natural light sources. Along each vertical scale the full range of luminance levels between maximum sunlight and minimum starlight are shown. The range of luminance levels produced by the moon at various altitudes and phases, and by natural starlight, are also indicated. "Open habitats" refer to situations where the substrate is not shaded by vegetation. "Closed habitats" refer to substrate luminance levels which would occur beneath a closed canopy woodland, which attenuates the incoming light by 100-fold. Maximum cloud cover is considered to reduce light levels ten-fold. From Martin 1990a.

among the Procellariiformes and Ciconiiformes nocturnal foraging may occur throughout the year, while among the waterfowl and shorebirds it is most likely to occur during the non-breeding season. Papers in this symposium by Brooke & Prince, McNeil and Owen discuss the nocturnal foraging of these groups in detail.

WHAT IS NIGHT TIME?

A particular difficulty in discussing nocturnal behaviour lies in the range of light levels which can occur at night and in the variability of night length. Figure 1 shows the range of light levels which can occur in the open and beneath a closed canopy woodland due to different natural sources of illumination. It can be seen that, although the times of sunset/sunrise or the end and start of civil twilight can be defined as the limits of night time, the naturally occurring light levels between such times can vary over a

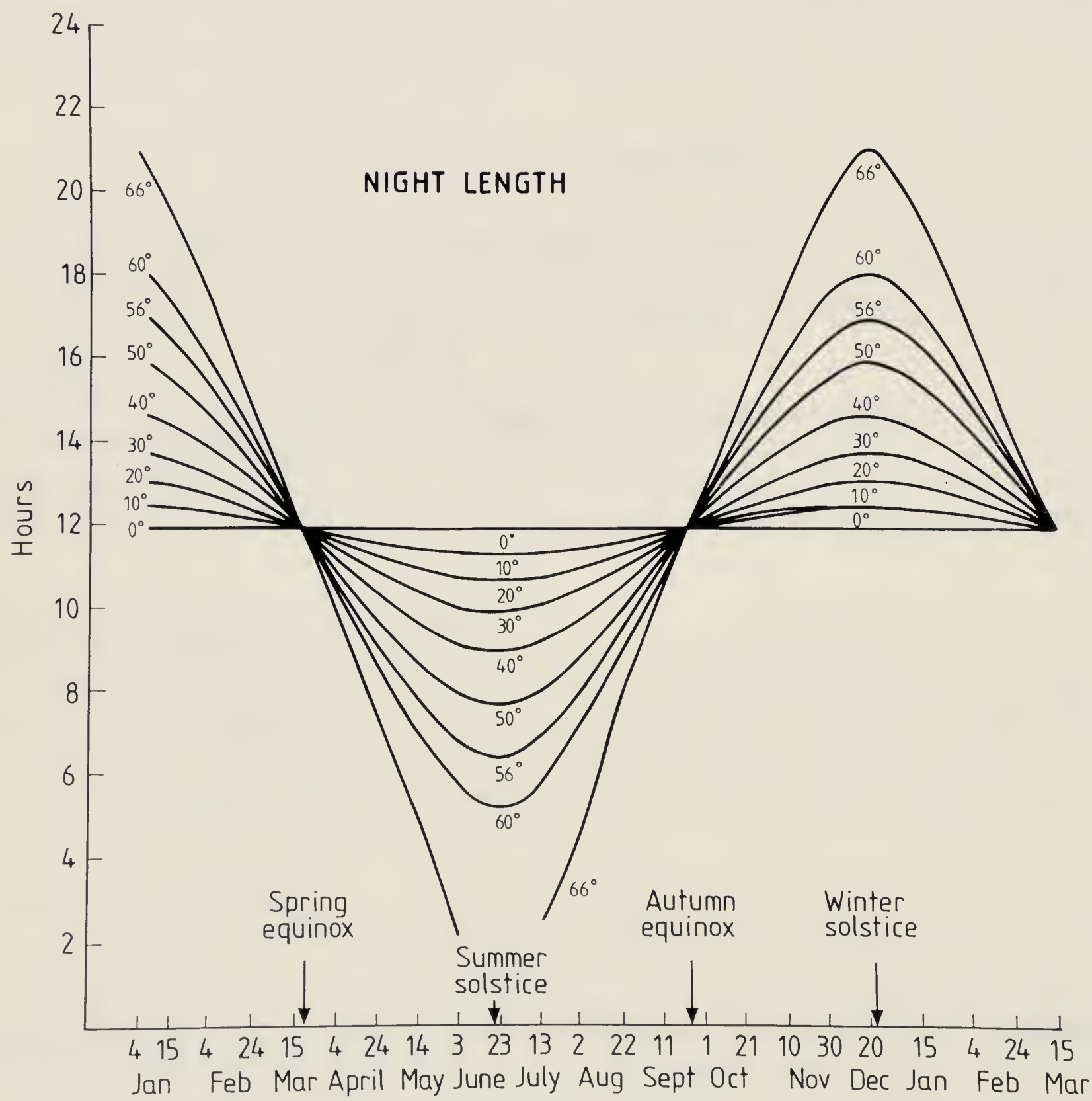


FIGURE 2 – The variation of night length (defined as sunset to sunrise) as a function of time of year, at different latitudes. (Dates refer to the Northern Hemisphere.) Each curve indicates how night length changes at a particular latitude over a 14 month period. Around the time of the summer solstice the sun does not set at latitudes above 66 degrees. Based upon data in The Astronomical Almanac (1988).

very wide range. For example, between sunset and sunrise natural illumination can vary over 9.0 log units (1,000,000,000-fold) depending upon the habitat type, and the presence of cloud and moon. It is noteworthy that maximum moonlight on a cloudless night in an open habitat can produce an illumination level equal to that of sunrise on a cloudy day within a woodland. Because of this variation light levels can vary as much by night as they do by day (Figure 1).

Figures 2 and 3 show that night length and the length of twilight vary markedly with both latitude and season. Species resident at the equator experience a quite different regime of night time to that experienced by those inhabiting temperate or higher latitudes. Figure 2 shows that night length at the equator is very uniform (the time between sunset and sunrise is to within one minute of 11 hours 53 minutes throughout the year), while towards the poles night length varies markedly with season. For example, at latitude 50 degrees night length can vary between 7.5 and 16 hours.

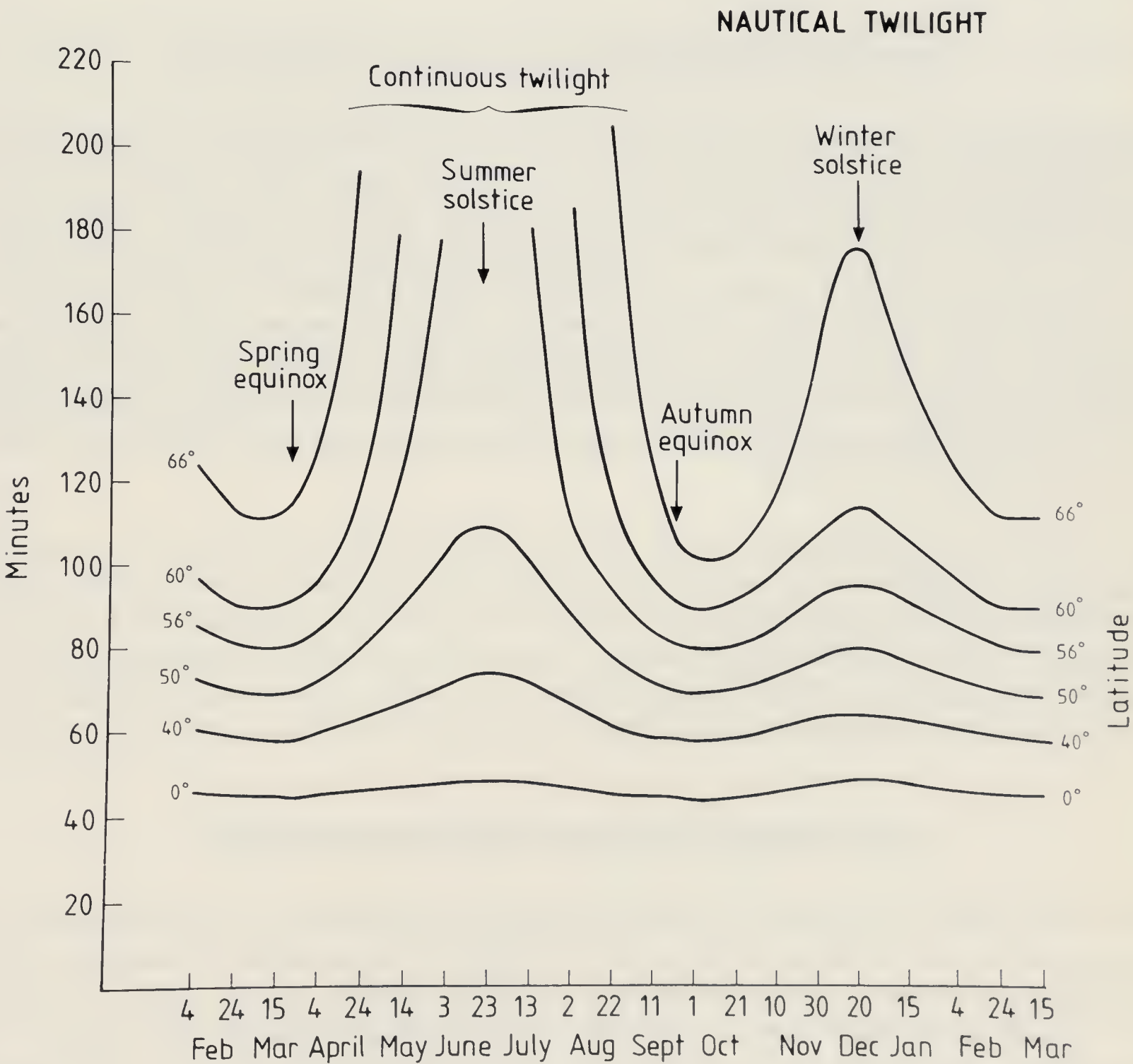


FIGURE 3 – The length of civil twilight (the period when the sun is between 0 degrees and 6 degrees below the horizon) as a function of the time of year at different latitudes. (Dates refer to the Northern Hemisphere.) Each curve indicates how the length of civil twilight changes at a particular latitude over a 14 month period. Around the time of the summer solstice at latitudes above 66 degrees twilight does not turn to night. Based upon data in The Astronomical Almanac (1988).

Figure 3 shows that the rate of change of light levels during the twilight period varies markedly with both latitude and season. Transition is most rapid at the equator and is the same throughout the year (civil twilight is always within 90 seconds of 21 minutes) while at latitude 66 degrees light levels may not fall below those of twilight for nearly 11 weeks around the time of the summer solstice. These facts should caution against anecdotal observations of what birds do "at night". In field observations of nocturnal behaviour, if light measuring devices are not available, it is necessary to record the presence/absence of the moon, cloud cover, latitude, date and time.

Observers should always be aware of the need to allow their own vision to fully dark adapt (which requires 40 minutes exposure to the ambient night time light level) before comparisons are made between what an observer can or cannot see compared with the presumed sensitivity of an animal under observation. Dark adaptation can raise the sensitivity of the vertebrate eye by over 10,000 fold compared to sensitivity at daylight levels (Barlow 1972).

SENSORY PROBLEMS OF NOCTURNAL BEHAVIOUR

Lessons learnt from the large body of data aimed at understanding the sensory bases of homing behaviour in birds (Keeton 1979, Papi & Wallraff 1982) suggest that there is unlikely to be a single sensory basis for nocturnal behaviour in birds. Rather, while a particular nocturnal activity may be dependent upon one primary cue, full understanding will probably demand an appreciation of how different cues are used in an integrated, often apparently redundant, manner. This is revealed particularly in investigations of the sensory bases of nocturnal behaviour of some owl species (Martin 1990a), in studies of nocturnal nest location by procellariiform seabirds (Brooke, 1990) and in consideration of the sensory cues which may be available to nocturnally migrating birds (Martin 1990b).

Studies of nocturnal foraging have indicated the importance of sensory capacities other than, or additional to, vision in the guidance of nocturnal behaviour. The senses of olfaction, hearing, taste and touch sensitivity seem to play a crucial role in nocturnal foraging. There is a clear need for further study of these sensory capacities and of the organs and receptors which mediate them. Information about these senses could usefully inform investigators of what birds do at night and of how and why they do it.

NOCTURNALITY, ECOLOGY AND CONSERVATION

All of the papers presented here demonstrate the importance of studying nocturnal behaviour for a full understanding of the ecology of many species. Brooke & Prince catalogue the diverse sources of information which must be pieced together to establish that many seabirds forage regularly, some perhaps exclusively, at night. They demonstrate clearly that to ignore these "unseen" activities is to ignore a vital aspect of these species' ecology. They also demonstrate the need to develop better techniques for following the behaviour of pelagic birds whether by day or night.

Both Owen and McNeil show clearly that, while nocturnal feeding may occur irregularly in many species and populations of shorebirds and waterfowl, it may neverthe-

less be of critical importance to the successful completion of the annual cycle. Thus opportunities to feed by both night and day, and perhaps even the specific protection of night time feeding areas, may be crucial for the conservation of populations. The efficiency of night time versus day time foraging in these birds, and the factors which lead some populations to feed at night are clearly worthy of investigation. The recent finding that some waterfowl populations may feed almost exclusively at night suggests that fundamental aspects of these birds' ecology have been inadequately addressed.

We hope that the questions raised in this symposium will encourage the most resolutely diurnal ornithologist to spare some thought for what birds do at night and to consider why and how they might do it.

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NOCTURNALITY IN SHOREBIRDS

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ABSTRACT. Most shorebird species of the order Charadriiformes forage both by day and night in temperate and tropical latitudes. Some species appear to use their daytime territory at night. In a few species display flights take place at dusk and at night. Some visually guided peckers and some long-billed tactile probers forage by the same preferred method both night and day. However, some birds change from visual to tactile foraging between day and night. The roles of moonlight and bioluminescence in prey detection are discussed. Nocturnal foraging appears induced by the need to avoid diurnal disturbance, including predation pressure, and/or to take advantage of prey that are more abundant or more easily available at night than during the day. Tidal cycle is important in influencing the period of feeding in many species. Day and night habitat segregation has been reported for wintering shorebirds. The conservation implications of nocturnal foraging and directions for further research are briefly discussed. **Keywords:** Nocturnality, night activity, night feeding, activity pattern, shorebirds, waders, feeding strategy, adaptation.

INTRODUCTION

This review discusses the occurrence of the three main types of nocturnal activity in shorebirds of the order Charadriiformes: foraging, display behaviour, and territoriality. The other major nocturnal activity which shorebirds exhibit, nocturnal migration, is not discussed.

NOCTURNAL DISPLAYS

In a small number of the more terrestrial shorebird species display behaviours, flights and calls, take place principally at dusk and occasionally during the night. Such species include the painted snipes *Rostratula* (Hayman et al. 1986), woodcocks *Scolopax* (Sheldon 1961, Krohn 1971, Stribling & Doerr 1985) and snipes *Gallinago* (Cramp & Simmons 1983). In Purple Sandpipers *Calidris maritima*, sexual activity has been recorded at all hours of day and night (Cramp & Simmons 1983). Stone-curlews *Burhinus oedicephalus* and Red-wattled Lapwings *Vanellus indicus* are vocal mainly at night (Cramp & Simmons 1983).

NOCTURNAL TERRITORIALITY

During the non-breeding season, many species of shorebird defend foraging territories (Myers et al. 1979) and Wood (1986) has shown that some Grey Plovers *Pluvialis squatarola* continue to use this foraging territory at night.

Furthermore, observations of Eurasian Curlews *Numenius arquata* (Cramp & Simmons 1983), Willets *Catoptrophorus semipalmatus* and Whimbrels *Numenius*

phaeopus (wintering in Venezuela) (unpublished data, B. Gagnon & R. McNeil) indicate that given territories defended during daylight were occupied by individuals of the same species during darkness. Finally, Cramp & Simmons (1983) mentioned that male Northern Lapwings *V. vanellus* continue visiting and defending their breeding territories on moonlit nights.

NOCTURNAL FORAGING

There are no reports that any shorebird forages exclusively at night. However, there are many reports of species regularly foraging both in the brightest parts of the day and during the night. Such species include oystercatchers *Haematopus* (Hulscher 1976), plovers *Pluvialis*, *Charadrius* (Evans 1979, Dugan 1981, Pienkowski 1983a, Robert et al. 1989), many *Calidris* species and most *Scolopacidae* (Evans 1979, Cramp & Simmons 1983, Robert et al. 1989), and stilts *Himantopus* (Robert & McNeil 1989). Other shorebird species are less likely to forage in full daylight but restrict their activity to twilight and night time. Such species include painted snipes (Cramp & Simmons 1983), woodcocks (Stribling & Doerr 1985, Granval 1988, Hirons 1988), Crab Plovers *Dromas ardeola* (Cramp & Simmons 1983), thick-knees *Burhinus* (Selous 1900, Cramp & Simmons 1983), Red-wattled Lapwings (Cramp & Simmons 1983), and a few snipe species *Lymnocryptes* and *Gallinago* (Cramp & Simmons 1983). Some species, such as Common Pratincoles *Glareola pratincola*, forage mainly by day but may occasionally feed at night, but only under bright moonlight conditions (Cramp & Simmons 1983).

Nocturnal foraging and latitude

Except for painted-snipes, crab-plovers and stone-curlews, nocturnal activities in shorebirds have been reported almost exclusively for birds wintering in coastal and estuarine habitats in temperate latitudes. However, recent studies in Venezuela have shown that some Neotropical residents and Nearctic winter migrants do feed at night in tropical environments (McNeil & Robert 1988, Robert & McNeil 1989, Robert et al. 1989). There seem to be only a few exceptions, e.g. the Purple Sandpiper in England and the Curlew Sandpiper *Calidris ferruginea* in South Africa were considered as not feeding at night during winter time (Feare 1966, Puttick 1979).

Foraging techniques at night

Two basic types of foraging techniques are used by shorebirds: visual searching for prey items, or indications of their presence on or near the surface; and probing with the bill for buried prey which are detected by tactile and taste cues. While some species may feed exclusively with one of these techniques (e.g. visual searching by plovers or tactile probing by Short-billed Dowitchers *Limnodromus griseus*), other species use the techniques flexibly, e.g. Semipalmated Sandpipers *Calidris pusilla* (Evans 1979). Some shorebirds may modify their foraging techniques between night and day. Thus oystercatchers (Hulscher 1976) and *Tringa* species (Evans 1979, Robert & McNeil 1989) are normally sight feeders during daylight but switch to tactile foraging at night. During daylight and on bright moonlit nights, Black-winged Stilts *H. himantopus* are usually visual peckers, but they use scythe-like sweeps of the bill (a tactile technique) on moonless nights or under lower moonlight conditions (Robert & McNeil 1989).

Moonlight and foraging at night

Since plovers, *Himantopus* and *Tringa* species forage either visually or by both sight and touch at night (Evans 1979, Robert & McNeil 1989), foraging methods do not prevent them foraging at low light levels. However, compared to species that feed mainly by touch (e.g. dowitchers *Limnodromus*), the activities of visually guided foragers should be relatively more affected by darkness (Dugan 1981, Pienkowski 1981b, Goss-Custard 1983). Pienkowski (1982, 1983a) concluded that plovers use sight as the main means of prey detection, even on dark nights, and showed that compared with daylight, Grey Plovers have lower pecking rates on dark moonless nights, but not on moonlit nights (Pienkowski 1982).

For some species, however, while the moon seems to influence nocturnal foraging activity, it does not appear that moonlight per se is the proximate factor. Thus, for most of the lunar month, Northern Lapwings and Eurasian Curlews forage by day and roost at night. For a few days around the full moon period, however, the situation is reversed even if the moon is not visible (Spencer 1953, Hale 1980). The significance of this is not known but it may reflect an increased activity of prey items influenced by the lunar cycle.

WHY FORAGE AT NIGHT?

There are two main hypotheses: (1) The "supplementary hypothesis", that night feeding occurs only when the daytime feeding has been inadequate to meet the birds' requirements. (2) The "preference hypothesis", that birds prefer to feed at night because it provides the most profitable, or safest, feeding opportunities.

The supplementary hypothesis

In support of the supplementary hypothesis are the following observations of factors which influence the occurrence of nocturnal foraging.

TIME OF YEAR AND LATITUDE. Activity patterns of birds are related to energetic needs which vary during the annual cycle. In temperate latitudes, energy requirements are generally higher during winter and most accounts of nocturnal shorebird feeding in northern Europe report that it is most intense during winter and less intense or absent in early autumn and spring (Goss-Custard 1969, Heppleston 1971, Goss-Custard et al. 1977, Pienkowski 1981a, 1982, Puttick 1984). At this time of year, there is less daylight available to search for food and prey availability may decrease because intertidal organisms move deeper within the sediment (and sometimes are less active) as temperature falls (Goss-Custard et al. 1977, Pienkowski 1982). In the tropics these factors do not apply, yet several shorebirds feed regularly at night (Robert & McNeil 1989).

In some tropical situations, e.g. mud flats in Mauritania, daytime prey abundance may be low. This is because during daytime the surface dries and invertebrates, forced to depths within the mud, may become unavailable to shorebirds. Thus, feeding in daylight alone is sometimes insufficient for these shorebirds to achieve their daily energetic needs (Engelmoer et al. 1984).

In addition, we can suspect that even in the tropics the occurrence of nocturnal feeding may be greater when migratory species have higher energetic demands (Myers

& McCaffery 1984). For instance, during the time of premigratory fattening, when re-fuelling at a stop-over place, or when landing after a long over-sea flight. In southern Portugal, Batty (1988) has reported that nocturnal feeding is common during autumn migration, rare in winter months (November-February), and more frequent in March.

THE TIDAL CYCLE. Tides may limit access to feeding sites regardless of prey abundance (Burger 1984). This factor affects particularly those shorebirds which feed at the intermediate and low intertidal zones and in estuarine environments (Evans 1976). However, even species not affected by tides may sometimes feed at night. For example, shorebirds feeding in coastal lagoons in northern Venezuela can feed all of the time, even during most high tides, yet these birds may feed by both night and day (Robert & McNeil, 1989).

The preference hypothesis

In support of the preference hypothesis are the following observations:

LUMINESCENCE. Pienkowski (1983a,b) suggested that shorebirds might take advantage of luminescent organisms at night. However, in the Chacopata Lagoon (north eastern Venezuela), no relationship was found between the presence or absence of bioluminescence and the types of nocturnal feeding methods (Robert & McNeil 1989). The relationship could be indirect at best if it were demonstrated that prey, e.g. fishes, on which *Tringa* and *Himantopus* species feed at night, are attracted by luminescent organisms.

ABUNDANCE OF PREY. Some species may take advantage of increased availability and activity of prey at night (Dugan 1981, Pienkowski 1983a,b, Townshend et al. 1984, Robert & McNeil 1989). It may even be advantageous for shorebirds to feed at night at sites and on prey that are not used during the day (Evans & Dugan 1984, Townshend et al. 1984, Robert & McNeil 1989, Robert et al. 1989).

At some sites, the abundance and/or activity of prey is higher at night than during daylight (Robert & McNeil 1989). Black-winged Stilts and *Tringa* species use such sites principally at night and seem to feed then on food items (fishes, *Pelecypoda* and Hemiptera) at least partly different from those they foraged for during daylight (Robert & McNeil 1989). The use of different day and night habitats might be a fundamental requirement for wintering shorebirds, at least in some regions.

DAYTIME DISTURBANCE. Nocturnal activities in shorebirds may be related to the avoidance of diurnal predators or other kinds of diurnal disturbance. The limited information that is available indicates that this may be the case in both northern latitudes and the tropics. In the Chacopata Lagoon (Venezuela), small bays surrounded by mangrove woodlands are used for feeding by shorebirds much less frequently by day than by night. This is in spite of the fact that they are very rich in prey at all times. During the day the birds congregate on vast, open mudflats, apparently to avoid predation by Peregrine Falcons *Falco peregrinus* (Robert et al. 1989). Also in the same lagoon, Wilson's Plovers *Charadrius wilsonia*, in spite of the *Uca* crab abundance, forage very little during daytime; daylight prey intake alone is insufficient to counterbalance their energy budget, and the fact that they forage mainly at night appears to be related to predator avoidance during daylight (Morrier & McNeil, in prep.).

In northeast Africa, Painted Snipes feed at times during the day if the area is undisturbed by humans and other mammals, though only where cover is plentiful (A.J. Tree, *vide* Cramp & Simmons 1983).

In the northern latitudes, Common Snipes *Gallinago gallinago* and Woodcocks switch from a woodland daytime feeding habitat in summer to night-time feeding pastures in winter (Dunford & Owen 1973, Grisser 1988, Hirons 1988). The switch to night feeding in the open habitats may reflect increased vulnerability to predators in these situations. According to Cramp & Simmons (1983), Pintail Snipes *Gallinago stenura* feed mainly at night but may feed during daytime, if undisturbed.

CONCLUSIONS

The habit of nocturnal foraging in shorebirds may be viewed as a behaviour that emerged in different groups of species for different reasons and whose occurrence is governed by a range of factors. For some of the more terrestrial species nocturnal foraging occurs regularly and may be preferred to feeding by day. For the majority of species and populations, however, it seems that foraging at night is less preferred and probably less efficient than foraging by day. However, the use of open habitats by these species, and their ability to locate prey by virtue of tactile cues, has given them the option of feeding at night should energetic demands not be satisfied by daytime feeding. Thus these birds have a flexibility in foraging strategy which few other avian groups possess. Nocturnal feeding is important for successful completion of the annual cycle in many populations of shorebirds and so should be taken into account in any conservation measures. The indication that some shorebirds feed nocturnally at sites and on prey that are not used during the day could lead to the protection of some wintering habitats less densely populated by shorebirds during the day, but more intensively used at night.

Many authors have dealt with time-activity and/or energy budgets of shorebirds. However, nobody seems to have taken nocturnal activities into account. Most information on the time and energy budgets of shorebirds needs to be revised having in mind their nocturnal activities.

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NOCTURNAL FEEDING IN WATERFOWL

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ABSTRACT. Feeding at night is a common activity among waterfowl Anatidae and a variety of feeding patterns has been recorded. Terrestrial herbivores (geese and swans) rarely feed at night but many duck species do, some species almost exclusively. Grazers are, however, not as selective at night. The only evidence from birds which pursue mobile prey, such as fish-eating ducks, indicates predominantly diurnal foraging. The reasons for nocturnal foraging that have been demonstrated or suggested include: (a) inability to gather sufficient energy in the short days of midwinter, (especially for herbivores and those whose feeding is restricted by the tide); (b) pressure from predators necessitating diurnal gregariousness away from feeding areas; (c) human disturbance; (d) energy conservation (concentration of heat generating activities to the cooler night time); and (e) matching foraging periods to the active times of prey.

Keywords: Waterfowl, Anatidae, nocturnality, foraging, energetics, time budget.

INTRODUCTION

Waterfowl Anatidae vary considerably in their tendency to forage at night. Taking examples from the whole range of species and habitats, this review shows that nocturnal foraging is related both to intrinsic and environmental factors. Table 1 summarizes the available quantitative data on nocturnal foraging in waterfowl in relation to diet and habitat type.

FORAGING AND HABITAT TYPE

Terrestrial habitats

Wildfowl which feed in these habitats are all herbivores, principally grazers. When grazing, geese are almost exclusively diurnal (review in Owen 1980) but this does not hold true for grazing ducks.

The reluctance of terrestrial geese to feed at night is illustrated by White-fronted Geese *Anser albifrons*. During the short days of midwinter in temperate latitudes these birds may forage for all of the daylight hours yet fail to balance their energy budget and lose body mass (Owen 1972). However, they do not feed at night to make good this deficiency. In contrast grazing ducks in similar circumstances may forage at night; Wigeon *Anas penelope* foraged for up to 40% of the night when their energy requirements were not met by daytime foraging (Mayhew 1988).

It is probably lack of light which inhibits night feeding in geese. Thus, the time of early morning departure of Barnacle Geese *Branta leucopsis* to their feeding grounds is delayed on overcast days but feeding by bright moonlight has been recorded (Ebbinge et al. 1975). Furthermore some species may be active at night under artificial lights (Forshaw 1983).

Estuarine habitats

On estuarine mudflats waterfowl tend to forage by both day and night. Wigeon and Brent Geese *Branta bernicla* feeding on mudflats in Denmark showed a near-identical foraging pattern by both day and night (Madsen 1988). Similar results have been found for Wigeon elsewhere (Mudge 1989 unpub., D.V. Bell unpub.). Time of day had little influence on the feeding activity of Snow Geese *Anser caerulescens* grubbing for roots in intertidal habitats. The feeding rhythm was apparently under the control of the tidal cycle. However, the same species showed a strong circadian pattern on an area not affected by tides and fed exclusively by day (Gauthier et al. 1988).

Marginal aquatic and shallow-water habitats

The majority of dabbling ducks *Anas* spp. largely feed in shallow water and at the land/water interface. These species are likely to feed by night but their behaviour is not uniform.

Some reports indicate that on the wintering grounds *Anas* species feed almost exclusively at night, for example, Teal *A. crecca* (Tamisier 1974, 1976, van Eerden 1984) and Pintail *A. acuta* (Tamisier 1976), while other studies indicate a high proportion of diurnal feeding in similar habitats. For example, Teal were reported to spend 51% (Zwarts 1976) and 23% (Quinland & Baldassarre 1984) of daylight foraging at times of high energy demand.

Mallard *A. platyrhynchos* spent 35% of the daylight period feeding, compared with 42% of the night (Jorde et al. 1983). In captivity the same species will feed by night and day but shows a preference for diurnal foraging (Figala et al. 1990). A close relative, the subtropical Laysan Teal *A. laysanensis*, is reported to feed only at twilight and at night (Moulton & Weller 1984). The Mottled Duck *A. fulvigula* spent 39% of daylight and 51% of night time feeding (Paulus 1988). Campredon (1981) reported that Gadwall *A. strepera* spent over 60% of the time foraging during both daylight and darkness. The herbivorous Wigeon, when feeding in these types of habitat, was reported to spend 74% of the night feeding (Campredon 1981).

The most carnivorous of the *Anas* ducks, the Shoveler *A. clypeata*, is reported to spend just over 12 hours feeding each day, sieving plankton from the water column; 94% of this is at night (Pirot & Pont 1987).

Deep water habitats

There is little information on the time budgets of swans (herbivores) when feeding in deeper water, but limited studies of Mute *Cygnus olor* and Bewick's *C. columbianus* Swans indicate that foraging is largely diurnal but may continue into darkness (Owen & Cadbury 1975).

In winter, diving ducks are generally found resting on water during the day; most species forage for a substantial proportion of each night. Thus Tufted Ducks *Aythya fuligula* were found to forage almost exclusively at night (Pedroli 1982). In the pre-breeding period Pochard *A. ferina* spent seven hours feeding, equally by night and day (Klima 1966). Ruddy Ducks *Oxyura jamaicensis* in Britain in winter have been found to spend less than 10% of the daytime but up to 91% of the night time foraging (B. Hughes pers. comm.). However, in North America this species spent only 58% of the night foraging (Bergan et al. 1989).

TABLE 1— Quantitative data on nocturnal foraging in wildfowl in relation to diet and habitat type in the non-nesting season. Because some studies were conducted over periods of varying daylength and means are not given, and others include a degree of interpolation, the proportion of the total feeding that takes place at night (calculated, in the absence of detailed data, on the assumption of equal periods of light and dark) are sometimes approximate. Where a ? follows the diet record, the diet was not determined in that particular study and the diet given is from other published sources. For diving species the feeding time includes the time spent submerged and the inter-dive interval during a foraging bout.

Species	Predominant diet	Habitat	Total time foraging (hr)	% nocturnal	Reference
<i>Anser albifrons</i>	vegetation	terrestrial	80	0	Owen 1972
<i>Anser caerulescens</i>	vegetation	terrestrial	13	0	Gauthier et al. 1988
	roots	intertidal	13	53	Gauthier et al. 1988
<i>Branta bernicla</i>	vegetation	intertidal	11.4	43	Madsen 1988
<i>Anas penelope</i>	vegetation	terrestrial	13	33	Mayhew 1988 *
	vegetation	marginal	13.5	74	Campredon 1981
	vegetation	intertidal	12.7	49	Madsen 1988
	vegetation	aquatic	13.4	53	Paulus 1984
<i>Anas strepera</i>	seeds	marginal	11	90	Tamisiair 1974
<i>Anas crecca</i>	grain	terrestrial	6	40	Jorde & Owen 1988
<i>Anas platyrhynchos</i>	seeds	marginal	10.3	56	Paulus 1988
<i>Anas fulvigula</i>	plankton	marg/aquatic	12.7	94	Pirot and Pont 1987
<i>Aythya ferina</i>	invertebrate?	aquatic	7	50	Klima 1966.
	seeds?	aquatic	6.8	24	Bergan et al. 1989
	mussels	aquatic	5.0	96	Pedroli 1982
	invertebrate?	aquatic	5.9	16	Bergan et al. 1989
<i>Bucephala albeola</i>	invertebrate?	aquatic	12.4	33	Bergan et al. 1989
<i>Oxyura jamaicensis</i>	omnivorous?	aquatic	13.7	91	B. Hughes unpubl. **
	omnivorous?	aquatic	8.8	58	Bergan et al. 1989

* studied by moonlight, but the species also feeds in darkness
** Only 20 hours monitored, 4 hours around dawn and dusk not included. The overall figure assumes crepuscular activity is intermediate between light and dark.

Bergan et al. (1989) also recorded the activities of three other diving ducks (Ring-necked Duck *Aythya collaris*, Lesser Scaup *A. affinis*, Bufflehead *Bucephala albeola*) in the same reservoir. All four species fed at night but the proportion of time varied, with the Ruddy Duck the most nocturnal (Table 1).

Sea ducks usually congregate in sheltered roosts at night and do not feed (Nilsson 1970, Sayler & Afton 1981), but there are exceptions. For example, Goldeneyes *Bucephala clangula* off the coast of Maine, USA, were recorded foraging at night by Jorde & Owen (1988).

Goosanders *Mergus merganser* and Red-breasted Mergansers *M. serrator* are fish eaters which hunt mobile prey. They usually locate fish from the surface by visual searching with the head immersed, although they can also feed in turbid water by probing under stones (Sjoberg 1988). On a Swedish river during the breeding season, both species feed predominantly in daylight, but have been recorded also feeding at night (Sjoberg 1985). However, these observations were made in May and June at latitude 64°N, when light intensities remain relatively high throughout the short night.

FACTORS AFFECTING THE DEGREE OF NOCTURNAL FORAGING

The incidence of nocturnal foraging in wildfowl varies markedly both between and within species and with habitat type. Some general patterns do, however, emerge and factors which may influence the degree of nocturnal foraging are discussed below.

Time of year

In temperate and higher latitudes day length varies markedly with season (see Martin & Brooke, this symposium). The daily energetic requirements of wildfowl also fluctuate through the annual cycle (review in Owen & Black 1990). The most demanding time of year for most temperate species is early spring (when night length still exceeds 12 hours) and when species undertake long migrations and also need to lay down body reserves on which they partially depend during nesting. There are few detailed studies, but it appears that energetic pressures may often necessitate both diurnal and nocturnal feeding at this time (Jorde & Owen 1988).

Potential predation

Among terrestrial geese and swans it seems clear that potential predation by mammals is a deterrent to night feeding. Even when birds are in negative energy balance they feed at night only in situations where predators are absent, such as a fox-free island (Ydenberg et al. 1984) or in semi-aquatic habitats (Lebret 1969, Gauthier et al. 1988). Night feeding also takes place when predators can perhaps be more readily detected, such as during moonlight, or in artificially lit areas (Ebbinge et al. 1975, Forshaw 1983).

On the other hand, predation by diurnal raptors has been suggested to account for nocturnal feeding in Teal and other dabbling ducks (Tamisier 1974, 1976, Pirot & Pont 1987). Tamisier argues that these ducks are forced to congregate in large, open areas, not suitable for feeding, when raptors are active, since their detection is better in such circumstances. However, Table 1 shows that this pattern is not predominant among *Anas* species. Some species feed for a considerable proportion of daylight

hours even though their energy requirements could be fulfilled solely by nocturnal feeding. It may be that differences in activity patterns relate to the prevalence of diurnal predators (Tamisier 1976). The energetic demands in different wintering areas are also clearly of relevance. Poysa (1987) found that Teal on a Finnish lake sacrificed vigilance scanning in favour of foraging as energy demands increased.

Human disturbance

Human disturbance, as it affects feeding opportunity, is often cited as one of the main reasons for nocturnality in ducks. Owen & Williams (1976) found that Wigeon fed by day and night in undisturbed areas but where feeding grounds were subject to disturbance they fed only at night. The amount of food in the guts of Wigeon shot at different times of day confirmed exclusive nocturnal feeding in two other sites (Owen 1973, D.V. Bell & Owen unpubl.).

However, where there was no daytime disturbance, 80-90% of the day was spent foraging (Owen & Thomas 1979, von Kanel 1981). Paulus (1984) found that hunting disturbance forced Gadwall to abandon marshes and spend the day on impoundments, where feeding opportunities were fewer, and to increase the proportion of nocturnal feeding. Belanger & Bedard (1990) found that human disturbance of Snow Geese caused an increase in energy demand; birds compensated by increasing nocturnal foraging.

Tidal cycle

In tidal areas surface feeders cannot reach food when mudflats are covered by deep water. Both Wigeon and Brent Geese regulate their activity according to the tidal cycle (Madsen 1988). Studying Snow Geese wintering in Quebec, Gauthier et al. (1988) showed that tides control the feeding cycle in estuarine areas and so night feeding occurs. On fields, however, night feeding is absent.

Food quality

Small herbivores, such as Wigeon and Gadwall, have relatively high energy demands and a fibrous diet of low calorific value and digestibility. These birds need to feed for 12-14 hours per day, necessitating at least some nocturnal foraging in winter. The larger size of grazing geese means that their relative energy demands are less.

Nevertheless, restriction to diurnal feeding causes loss of body mass during the shortest and coldest days. When feeding on an energy-rich diet of grain, however, Canada Geese *Branta canadensis* spend only around three daylight hours on the feeding fields (Raveling et al. 1972). Similarly, grain-eating Mallard and Pintail obtain most of their daily needs in two to four hours of daylight and do not feed at night (Jorde et al. 1983, Thomas 1981).

Body size

Body size, as it affects existence energy demands, influences the amount of time required for feeding. Bergan et al. (1989) attributed the varying degree of nocturnality in diving species to energetic differences. The smallest species, the Bufflehead, spent most time feeding overall and was most nocturnal (Table 1). Moreover, the smaller females spent more time foraging at night than males.

Ambient temperature

Low temperatures may act both to increase and decrease the tendency towards night feeding. Thus, Brodsky & Weatherhead (1984) found that the proportion of time Black Ducks *Anas rubripes* spent resting increased at low temperatures, and that birds rested all night. They argued that the energy costs of feeding exceed the benefits at very low temperatures.

Alternatively it is perhaps advantageous for ducks to concentrate heat-generating activities in the cooler night (Jorde & Owen 1988). The heat generated by foraging and digestion may help to maintain temperature balance during the night. This may be important for tropical or subtropical species, such as the Laysan Teal, which does not forage in the heat of the day. Moulton & Weller (1984) argue that, if daytime feeding occurred at these low latitudes, energy would have to be expended in dissipating the heat such activities generated.

Sensory factors

Birds using visual cues to locate and/or select their prey are clearly at a disadvantage in poor light. Nilsson (1970) suggested that sea ducks pursuing mobile prey should feed diurnally, whereas those preying on sedentary animals such as shellfish could feed by day and night. The evidence is sparse, but fish-eating ducks favour daylight foraging; Sjoberg (1985) found that at the beginning of the breeding season, Goosander exhibited a bimodal feeding rhythm, with morning and evening peaks. Later, in the spawning period of the main prey, the river lamprey *Lampetra fluviatilis*, a nocturnal species, foraging occurred only in late evening. Thus the Goosanders matched their activity to that of their prey.

There is evidence that Barnacle Geese cannot be as selective when grazing at night (R.H. Drent pers. comm.). However, whether night feeding in grazing geese is less efficient because of this has not been tested experimentally.

CONCLUSION

Nocturnal foraging is a common activity of waterfowl; most ducks and swans feed at night to some extent and a few species may do so almost exclusively. The reasons for nocturnality are, however, many and the factors which may control its incidence complex. In the majority of wildfowl, nocturnal foraging seems to be a flexible response to a variety of factors rather than a fixed pattern of behaviour.

I have found only one example - the matching of Goosander activity with that of its nocturnal prey - where night-time feeding (albeit in conditions of reasonable light at high latitude in summer) has been proven to be advantageous. Thus, although common, foraging by night is perhaps most appropriately viewed in the majority of waterfowl as a less preferred strategy than feeding by day. It occurs only when energetic demands or predatory pressures dictate. However, we do not know why nocturnal feeding should be so prevalent in some species of diving ducks.

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NOCTURNALITY IN SEABIRDS

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ABSTRACT. Although there is some direct observational evidence of nocturnal feeding in seabirds, most evidence is circumstantial - absence from the colony by night, prey species found near the sea surface only by night, and, compared with daylight, a higher proportion of the night-time hours spent on the water and a lesser proportion in flight (activity recorder data). Species within three orders, Sphenisciformes, Procellariiformes and Charadriiformes, are active at the colony exclusively by night, probably mainly to reduce the risk of predation.

Keywords: Nocturnality, seabird, petrel, albatross, squid, radio-tracking, colony activity.

INTRODUCTION

Nocturnal activity in seabirds is considered here under two headings: feeding and attendance at the colony. We consider the evidence that these activities do indeed occur at night and the reasons why such nocturnal behaviour may be favoured. Discussion is restricted to species that are habitually active at night. Occasional instances of diurnal activities being completed at night are ignored.

NOCTURNAL FORAGING

Several types of evidence show that certain seabird species regularly forage at night. Every type of evidence may not be available for all species. Much evidence is circumstantial rather than direct.

Direct observation

When birds are reported to gather to feed at night beside a floodlit ship (e.g. Boswall 1960, Harper 1987), it is certainly possible that these are diurnal feeders exploiting a man-made opportunity. With this caveat the best direct evidence comes from Harper's (1987) observations of 20 species of Southern Ocean procellariiforms, of which 13 were seen feeding at night, five exclusively so. Other, essentially casual, observations of nocturnal feeding refer primarily to procellariiforms (Bourne 1955, Gould 1967) and to Sooty Terns *Sterna fuscata* (Gould 1967).

Evidence by default

This evidence takes two forms. The first accrues when species have (virtually) never been seen feeding by day. While it is difficult to make this evidence rigorous the conspicuous rarity of *any* daytime observations of feeding gadfly petrels *Pterodroma* spp. strongly hints at nocturnal feeding by these birds. The second strand of evidence comes from high latitude species, which during mid-winter enjoy little or no daylight, and primarily applies to northern species such as auks *Uria* spp. off northern Norway (Brown 1985) and north of the Bering Strait (Harrison 1983), and to Ivory Gulls

Pagophila eburnea scavenging in the wake of polar bears *Ursus maritimus* in winter (Bateson & Plowright 1959).

Activity patterns

In certain species both members of the pair are present at the colony by day. There is then a dusk exodus, followed by a dawn return and a strong presumption that feeding is mainly nocturnal. Such species include Swallow-tailed Gull *Creagrus furcatus* (Harris 1970), Red-legged Kittiwake *Rissa brevirostris* (Hunt et al. 1981) and, to a lesser degree, Black-legged Kittiwakes *R. tridactyla* (Myres 1963). In the last species preliminary radiotracking observations at the Isle of May, Scotland, confirm departures from the colony at night (S. Wanless & M.P. Harris, pers. com.). However, these colony activity patterns can be misleading. Thus, during their pre-laying cycles of colony attendance, Guillemots *Uria aalge* may be ashore for three consecutive days and absent during the intervening nights, but regular weighings of identified individuals suggested the nights were not used for feeding (B.J. Hatchwell, pers. comm.).

Diet

Extensive circumstantial evidence of nocturnal feeding comes from diet studies where the food identified is more likely to be available at or near the sea surface by night.

SPHENISCIFORMES. The possibility that King Penguins *Aptenodytes patagonicus* feed at night is raised by Adams & Klages' (1987) study at Marion Island, where the main prey were myctophids (lantern fish), which surface at night (Croxall et al. 1988). However, results from deploying activity recorders on King Penguins are contrary (see below).

PROCELLARIIFORMES. Since Imber's (1973) paper on Grey-faced Petrels *Pterodroma macroptera gouldi*, numerous studies have documented the importance of squid in the diet of procellariiforms (Prince & Morgan 1987). Since squid are rarely close to the surface by day and these birds do not dive deeply, the general presumption has been that squid are caught by the petrels at night when they regularly reach the surface (Hardy 1956). There is still, however, considerable uncertainty about the circumstances of capture. Imber suggested the birds might particularly catch bioluminescent squid but Clarke et al. (1981) pointed out that the proportions of bioluminescent and non-bioluminescent squid in albatross diets roughly equalled the relative abundance of the two categories of squid.

Lipinski & Jackson (1989) reported that the squid eaten by Benguela seabirds are predominantly, but not exclusively, species which float (rather than sink) after death. If the birds are generally taking dead squid, the prey would be available by day and night.

Can we deduce, from the size of squid eaten, whether they might have been caught alive, or were they so large as to preclude live capture? Grey-headed Albatrosses *Diomedea chrysostoma* and Black-browed Albatrosses *D. melanophrys* feed their chicks on entire squid up to 410 g weight, and therefore small enough to be swallowed whole (Prince 1980). Also during the five-month chick-rearing period, about 90% of the squid component of Grey-headed Albatross diets is a single species *Martialia hyadesi*. Such squid die principally after (synchronous) spawning, and so it is unlikely that dead squid would be consistently available over such a long period. In any case

Martalia hyadesi lacks a buoyancy mechanism, and so would not float when dead (P.G. Rodhouse, pers. comm.). Further supporting live prey capture is Harper's (1987) account of how readily albatrosses and gadfly petrels *Pterodroma* can disable squid. Nevertheless some squid beaks found in albatross stomachs certainly do derive from squid too large to be taken live. In these cases the albatrosses scavenged dead squid or perhaps fed on the regurgitates of sperm whales *Physeter macrocephalus* (Clarke et al. 1981).

The specialist squid eaters, and therefore nocturnal feeders, are the albatrosses *Diomedea* and the gadfly petrels. But there is also evidence of nocturnal feeding in other species such as the Northern Fulmars *Fulmarus glacialis*, Bulwer's Petrels *Bulweria bulwerii* and Wedge-rumped (=Galapagos) Storm Petrel *Oceanodroma tethys* (Harris 1969a, Harrison et al. 1983, Furness & Todd 1984).

PELECANIFORMES. Red-footed Boobies *Sula sula* take significant quantities of squid, up to about 20% of the diet by weight (Diamond 1974), and may hunt at night (Murphy 1936). The Brown Booby *Sula leucogaster* may also be a nocturnal hunter (Nelson 1978).

CHARADRIIFORMES. There is little firm dietary evidence for nocturnal feeding by alcids, although the possibility certainly exists for those species feeding on vertically migrating plankton e.g. Little Auk *Plautus alle* catching copepods (Bradstreet & Brown 1985). Most gulls and terns are diurnal but there is suggestive evidence that the two Kittiwake species feed at night, Red-legged on myctophid fish (Hunt et al. 1981) and Black-legged the vertically migrating euphausiid *Thysanoessa inermis* (B. Zonfrillo, pers. comm.). Similarly the diet of the Swallow-tailed Gull is fish and squid, the latter at least being more readily caught at night (Hailman 1964, Harris 1970). Thus for these three gull species the dietary data reinforce the colony activity data (above) in pointing towards nocturnal feeding. Among terns, Fairy Terns *Gygis alba* on Christmas Island (Pacific) take 40-50% squid (by volume), which Ashmole & Ashmole (1967) believed were caught at night. Finally there are reports of Sooty Terns regurgitating food items likely to have been caught after dark (Bruyns & Voous 1965, Dinsmore & Robertson 1972).

Activity recorders

These devices have been deployed with increasing success on penguins and procellariiforms (Croxall et al. 1988, Prince & Francis 1984).

The data output from penguin studies has been a sequence of diving depths over the duration of a foraging trip. Macaroni Penguins *Eudyptes chrysolophus* studied by Croxall et al. (1988) were regularly at sea by night. They continued to dive then, and at a higher rate than by day. However, at night they rarely dived below 20 m since euphausiid prey was closer to the surface. Additional data (J.P. Croxall pers. comm.) indicate that diving at night increases as chicks grow and require more food. In contrast Gentoo Penguins *Pygoscelis papua*, also feeding on krill, are rarely at sea during the night (Williams & Rothery in press). Comparable data on King Penguins in South Georgia (G.L. Kooyman, pers. comm.) suggest that most feeding dives are diurnal. However, the birds regularly dive below 150 m, to depths where, compared with the surface, light levels are reduced by a factor of at least 1 million-fold (Moss 1980). In other words the penguins are hunting where light levels are comparable with those prevailing at the surface at night (see Martin & Brooke this symposium).

Activity recorders used on albatrosses have revealed the proportion of time spent on the water by day and night. The main finding is that Wandering, Black-browed and Grey-headed Albatrosses spent from three to 13 times more time on the sea by night than by day (Prince & Morgan 1984). Since these large albatrosses must alight on the water to feed, the implication is that feeding is mostly nocturnal. Whether feeding is concentrated around the twilight periods (part of which were registered as night on the recorders) or occurs throughout the night is not known.

Radiotracking

Jouventin & Wiemerskirch (1990) found that satellite-tracked Wandering Albatrosses *Diomedea exulans* flew about four times as far by day as by night and possibly fed during periods on the water; therefore mainly at night. In contrast, radiotracked Black Petrels *Procellaria parkinsoni* attained mean flight speeds three times higher by night (Scofield 1989). The implication, that night time was used mainly for travelling between food-rich regions was supported by patterns of signal loss. There was little loss by night but intermittent brief loss by day, suggesting total immersion for feeding.

DISCUSSION OF NOCTURNAL FORAGING

Although much of the evidence discussed above is circumstantial some general trends can be discerned: (1) Nocturnal feeders tend to feed offshore rather than inshore. (2) There is generally better evidence for nocturnal feeding by tropical and Southern Hemisphere species than for cool-water northern species. (3) The habit is often associated with a diet of squid caught in the open ocean. Consequently much of the data relates to those squid-eating specialists, the Procellariiformes, which have radiated abundantly in the Southern Hemisphere. Whether these trends reflect fundamental differences in northern and southern marine ecosystems, with squid more important in the latter, is an intriguing question.

Why feed at night?

The principal factor promoting nocturnal feeding is doubtless that there is, for the seabirds concerned, more food available to be caught at night. The main factor responsible for increasing prey availability is vertical migration of planktonic and mesopelagic animals (Hardy 1956).

Another factor promoting nocturnal feeding could be lower competition for available food. The reduction could obtain on a daily basis. Thus Harris (1970) wondered whether Swallow-tailed Gulls fed at night to avoid competition for similar prey from Red-billed Tropicbirds *Phaethon aethereus*, although Hailman (1964) and Snow & Nelson (1984) argue that kleptoparasitic attacks by frigatebirds *Fregata spp.* may have led to nocturnal activity in this gull. Alternatively, on a seasonal basis a nocturnal feeder will potentially experience maximum feeding time during winter. This could increase the benefits of rearing a chick in winter, and any species that rears its young then stands to reap the supplementary advantage of breeding at a season when abundant summer-breeding seabirds are not also foraging for their chicks and indeed may have migrated to the other hemisphere. All winter-breeding seabirds of temperate latitudes (the species rearing chicks at the winter solstice are King Penguins and procellariiforms of the genera *Diomedea*, *Pterodroma* and *Procellaria*) are species where nocturnal feeding is suspected.

NOCTURNAL ACTIVITY AT THE COLONY

Species in three seabird orders are active at the colony only by night. Although these species may attend nests at night they do not necessarily feed at night and vice versa.

Sphenisciformes

The only nocturnal penguin is the Blue Penguin *Eudyptula minor* of New Zealand, southern Australia and adjacent islands (Serventy et al. 1971). Although tempted to relate their nocturnal habit to the fact that this is the smallest penguin species, we do not know whether diurnal predation by skuas around southern New Zealand and by the indigenous land mammals of Australia has promoted nocturnality.

Charadriiformes

In the Atlantic all alcids are diurnal, whereas in the Pacific there are both diurnal and nocturnal species. Why there should be this difference between oceans is unknown. The nocturnal species are Rhinoceros Auklet *Cerorhinca monocerata*, Cassin's Auklet *Ptychoramphus aleuticus*, Whiskered Auklet *Aethia pygmaea*, Xantus' Murrelet *Synthliboramphus hypoleuca*, Craveri's Murrelet *S. craveri*, Ancient Murrelet *S. antiquus*, Crested Murrelet *S. wumizusume*, Marbled Murrelet *Brachyramphus marmoratus* and Kittlitz's Murrelet *B. brevirostris* (Bent 1919, Sealy 1976, Asbirk 1979, Manuwal 1979, Murray et al. 1983).

Procellariiformes

The procellariiforms are variously diurnal, crepuscular or nocturnal in a pattern broadly related to body size. Fourteen of the largest species, those belonging to the albatross family Diomedidae, are exclusively diurnal. The smallest species, the four diving petrels of the Pelecanoididae and the 20 storm petrels of the Hydrobatidae, are nocturnal with one exception, the Wedge-rumped Storm Petrel. Greatest variation is evident among the Procellariidae (Table 1), where some trends can be discerned. The large powerful giant petrels *Macronectes* spp. are diurnal. So too are the species of highest latitudes, fulmars (both species), Antarctic Petrel *Thalassoica antarctica*, Snow Petrel *Pagodroma nivea* and Cape Pigeon *Daption capense*. Since they breed in conditions of almost continuous daylight the nocturnal habit would offer no protection from predation. Instead they must rely on alternative protection, skilled vomiting and, usually, cliff nesting sites. The mid-latitude species include none that are wholly diurnal, but some that are crepuscular. The tropical procellariids include a mix of diurnal, crepuscular and nocturnal species.

Why attend colonies at night?

This brief survey strongly suggests that predation is the principal factor promoting nocturnality at petrel's breeding sites. The smallest and most vulnerable species are almost universally nocturnal; the largest, least vulnerable species are diurnal. Only among species of intermediate size is there much variation, presumably in response to local predation pressure e.g. Audubon's Shearwater *Puffinus lherminieri* diurnal in the Galapagos (Harris 1969b) but nocturnal in the Seychelles (personal observation). It is also interesting that the diurnal species, such as the Phoenix Petrels *Pterodroma alba* and Christmas Shearwaters *Puffinus nativitatis*, tend not to nest in burrows, presumably because the low level predation that permits diurnality also obviates the need for nocturnal nest in a protective burrow.

TABLE 1 – Tabulation of the breeding latitude, season and period of daily activity at the colony for members of the Procellariidae. Species arranged in taxonomic order. Activity abbreviations: D - diurnal, C - crepuscular, N - nocturnal. Subsidiary periods of activity in brackets. C? = possibly active crepuscularly. N? = possibly active nocturnally. Season of breeding not specified for species nesting entirely within the tropics. Otherwise Spr = main laying period between winter solstice and spring equinox, Sum = main laying period between spring equinox and summer solstice, Aut = main laying period between summer solstice and autumn equinox, and Win = main laying period between autumn equinox and winter solstice. Principal sources: Serventy et al. 1971; Harrison 1983; personal communications from M.J. Imber and authors' knowledge of species concerned.

Species	Breeding latitude	Activity at colony	Breeding activity
<i>Macronectes halli</i>	44-54°S	D	Sum
<i>M. giganteus</i>	47-70°S	D	Sum
<i>Fulmarus glacialis</i>	48-80°N	D	Sum
<i>F. glacialoides</i>	54-70°S	D	Sum
<i>Thalassoica antarctica</i>	c.70°S	D	Sum
<i>Daption capense</i>	44-70°S	D	Sum
<i>Pagodroma nivea</i>	54-70°S	D	Sum
<i>Pterodroma macroptera</i>	35-50°S	N	Win
<i>P. aterrima</i>	21°S	N?	n/a
<i>P. lessoni</i>	47-54°S	N	Sum
<i>P. hasitata</i>	19°N	N	n/a
<i>P. cahow</i>	32°N	N	Spr
<i>P. incerta</i>	37-40°S	N	Spr
<i>P. rostrata</i>	9-22°S	N	n/a
<i>P. alba</i>	0-30°S	D	Variable
<i>P. inexpectata</i>	47-48°S	N	Sum
<i>P. solandri</i>	32°S	D/C/N	Win
<i>P. brevirostris</i>	37-49°S	N	Sum
<i>P. ultima</i>	20-28°S	D	?
<i>P. neglecta</i>	24-34°S	D/C/N	Variable
<i>P. magentae</i>	44°S	N	Sum
<i>P. arminjoniana</i>	9-27°S	D/C	Variable
<i>P. mollis</i>	37-50°S	N	Sum
<i>P. feae</i>	16-32°N	N	Win
<i>P. madeira</i>	32°N	N	Aut
<i>P. barau</i>	20-21°S	C/N	n/a
<i>P. phaeopygia</i>	0-22°N	N	n/a
<i>P. externa</i>	29-34°S	N	Sum
<i>P. cooki</i>	33-36°S	N	Sum
<i>P. defillipiana</i>	26-34°S	C/N?	Spr
<i>P. leucoptera</i>	33°S	N	Sum
<i>P. brevipes</i>	18°S	N	n/a
<i>P. hypoleuca</i>	28°N	N	Spr
<i>P. nigripennis</i>	21-44°S	D/C/N	Sum/Aut
<i>P. axillaris</i>	44°S	N	Aut
<i>P. longirostris</i>	34°S	N	Sum
<i>P. pycrofti</i>	35-37°S	N	Sum
<i>Pseudobulweria macgillivrayi</i>	18°S	N	n/a
<i>Halobaena caerulea</i>	47-56°S	N	Sum

TABLE 1 – Continued

Species	Breeding latitude	Activity at colony	Breeding activity
<i>Pachyptila vittata</i> (incl. <i>salvini</i> & <i>desolata</i>)	37-67°S	N (C)	Spr/Sum
<i>P. turtur</i> (incl. <i>crassirostris</i>)	36-53°S	N (D/C)	Sum
<i>P. belcheri</i>	47-52°S	N	Sum
<i>Bulweria bulwerii</i>	9°S-38°N	N	Sum
<i>B. fallax</i>	13°N?	?	?
<i>Procellaria cinerea</i>	37-52°S	C/N	Win
<i>P. aequinoctialis</i>	37-54°S	C/N	Sum
<i>P. parkinsoni</i>	36°S	N	Sum
<i>P. westlandica</i>	42°S	N	Win
<i>Calonectris leucomelas</i>	24-42°N	C?/N	Sum
<i>C. diomedea</i>	16-41°N	C/N	Sum
<i>Puffinus creatopus</i>	34-38°S	N	Aut
<i>P. carneipes</i>	32-41°S	C/N	Sum
<i>P. gravis</i>	37-52°S	C/N	Sum
<i>P. pacificus</i>	30°S-28°N	C/N	Variable
<i>P. bulleri</i>	35°S	N	Sum
<i>P. griseus</i>	35-55°S	C/N	Sum
<i>P. tenuirostris</i>	35-42° S	N	Sum
<i>P. heinrothi</i>	5° S?	?	?
<i>P. nativitatis</i>	27°S-26°N	D/C	Variable
<i>P. puffinus</i>	38-64°N	N	Sum
<i>P. gavia</i>	34-41° S	N	Sum
<i>P. huttoni</i>	42°S	N	Sum
<i>P. newelli</i>	22°N	N	n/a
<i>P. opisthomelas</i>	28-29°N	N	Spr/Sum
<i>P. auricularis</i>	19°N	N	n/a
<i>P. assimilis</i>	50°S-38°N	N	Spr
<i>P. lherminieri</i>	21°S-28°N	D or N	Variable

Nocturnal activity at the breeding site potentially offers another advantage, that of efficient division of the day's 24 hours between feeding and nesting. This putative advantage applies most forcefully to species that forage by day and visit their colony at night (e.g. most shearwaters) and those which feed at night and visit nests by day (e.g. most albatrosses). It may also influence the daily cycle of other species (e.g. *Pterodroma* spp.) which, classified as crepuscular or nocturnal in Table 1, are actually most active at the colony around dusk. (No species appears to have its main period of colony activity at dawn.) After a period of dusk activity there would remain several hours of night for the birds to fly to sea and forage in the hours immediately preceding dawn when vertically-migrating marine organisms are closest to the surface (Hardy 1956).

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NOCTURNALITY, LONG-DISTANCE MIGRATION, AND ECOLOGICAL BARRIERS

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ABSTRACT. We argue that nocturnal migration is especially advantageous when birds must make long, nonstop flights over ecological barriers. Because energetic considerations become especially crucial at those times, we expected to find differences in the behavior of migrants before and after crossing the Gulf of Mexico. A positive relationship between energy reserves and the likelihood of nocturnal migration among captive Indigo Buntings *Passerina cyanea* existed only in fall, i.e. before trans-Gulf migration. Further, daytime flights of migrating passerines in relation to the Gulf of Mexico were observed after, not before, trans-Gulf migration. We propose that populations of long-distance migrants respond to an ecological barrier by increasing the “margin of safety” associated with certain phenotypic traits, including fat stores, orientation, and the diel timing of migration. The probability that a certain trait will permit an individual to survive reflects both the phenotypic level of the particular trait and the timing and magnitude of the environmental demands on the trait that the individual happens to encounter.

Keywords: Migration, Gulf of Mexico, energetics, orientation.

INTRODUCTION

Several hypotheses have been advanced to explain nocturnal migration, e.g. the need to forage during daylight, predator avoidance, and the avoidance of atmospheric turbulence (Evans, 1985, Kerlinger & Moore 1989, Martin 1990a). If natural selection has maximized the distance a bird travels per unit of time and energy expended (Alerstam & Lindstrom 1990), migrants should fly at times of the day and at heights where travel is least costly, most rapid, and safest. We have argued that atmospheric structure and the nutritional demands of migration are primary selective pressures that have shaped the diel timing of migratory flights (Kerlinger & Moore 1989).

We now explore the question of nocturnal migration in relation to long, nonstop flights over ecological barriers. Most long-distance migrants must cross at least one barrier during their migration (Alerstam 1981). Many of the adaptations that have evolved to meet the energetic demands of migration are probably critical when birds must cross deserts, mountains, oceans, or icefields (Alerstam 1981, 1990). If flying at night increases foraging time in relation to energetic demand (e.g. Lank 1989) and reduces the energy expenditure of long-distance migration (e.g. Moore & Kerlinger 1989), despite “problems” associated with flying at night (Martin 1990a,b), nocturnal flight should be especially advantageous when a migrant confronts an ecological barrier.

A prominent feature of the Nearctic-Neotropical migration system is the movement of landbirds across the Gulf of Mexico. Although specific routes may vary within and among species (Rappole et al. 1979), most migrant landbirds that breed in eastern North America make the nonstop flight (18-24 hours) of over 1000 km each spring and

fall (Buskirk 1980). If overcoming this barrier represents a significant "threat" to a successful migration, the behavior of passage migrants about to cross the Gulf of Mexico should differ from the behavior of birds that have crossed the barrier (see Alerstam 1990).

First, we examine the amount and orientation of migratory activity (nocturnal restlessness) among captive Indigo Buntings *Passerina cyanea* in relation to their energetic condition before and after crossing the Gulf of Mexico. If nocturnal migration is advantageous in relation to ecological barriers, birds about to cross the Gulf of Mexico in fall should do so only at night, whereas spring birds that have essentially completed a trans-Gulf flight when they stop along the coast should be more likely to depart during the day. Once the barrier is crossed, the likelihood of migration should depend less on the bird's energetic state.

Second, we illustrate our expectation that populations of migrants should increase the "margin of safety" associated with phenotypic traits, such as fat stores, orientation mechanisms, and the diel timing of migration, in response to an ecological barrier. Periods of stringency characterized by heightened energy demand coupled with an increased possibility that migrants will not meet en route contingencies selects for nocturnal migration.

METHODS

Cage-orientation experiments were conducted in April 1986 with migratory passerines that had stopped along the coast of Louisiana following a trans-Gulf flight (see Moore 1986, 1990), and in late September 1987 with birds that had stopped on Dauphin Island, Alabama, prior to trans-Gulf migration. Sufficient data to compare orientation behavior between spring and fall is available for Indigo Buntings. After migrants were captured using 12 m mist-nets, we recorded body mass and scored subcutaneous fat deposits according to Helms & Drury (1960), then held individuals in captivity until they were placed in Emlen orientation cages for two hours beginning at sunset the day of their capture. The nocturnal restlessness of captive migrants provides a conveniently measured index of migratory readiness (Berthold 1975) and was quantified according to Moore (1980). Individuals were assigned an energetic condition (lean or fat) based on fat scores. "Lean" birds were essentially fat-free, whereas "fat" birds were at least 15% - 20% heavier than fat-free mass. This difference translated approximately to > 550 km flight distance under still-air conditions (Pennycuick 1969).

RESULTS

All but four of the Indigo Buntings tested in spring ($N = 25$) were lean (fat score ≤ 1) birds, yet only 2 individuals failed to display nocturnal activity during the test period. Too few fat birds were tested to determine whether they produced more activity than lean birds on a nightly basis. Mean spring activity was oriented in a seasonally appropriate northward direction (Figure 1). Birds tested in autumn ($N = 31$) were more evenly distributed among fat classes, and individuals with fat scores ≤ 2 ($N = 17$) were largely inactive at night. The orientation of those birds that did produce migratory activity ($N = 5$) was either uniformly distributed or just as likely to be directed north as south (Figure 1). When birds given fat scores ≤ 3 ($N = 14$) were tested, the amount

of nocturnal cage activity increased dramatically, only one bird was inactive, and migratory activity was oriented southward (Figure 1). Indigo Buntings that scored 3 fat were, on average, 4.1 grams heavier than fat-free birds ($\bar{x} = 12.5$ g). Assuming the difference reflects fat deposition, a bird could travel approximately 1090 km on that "fuel" level, which is sufficient to reach the Yucatan Peninsula from Dauphin Island under still air conditions.

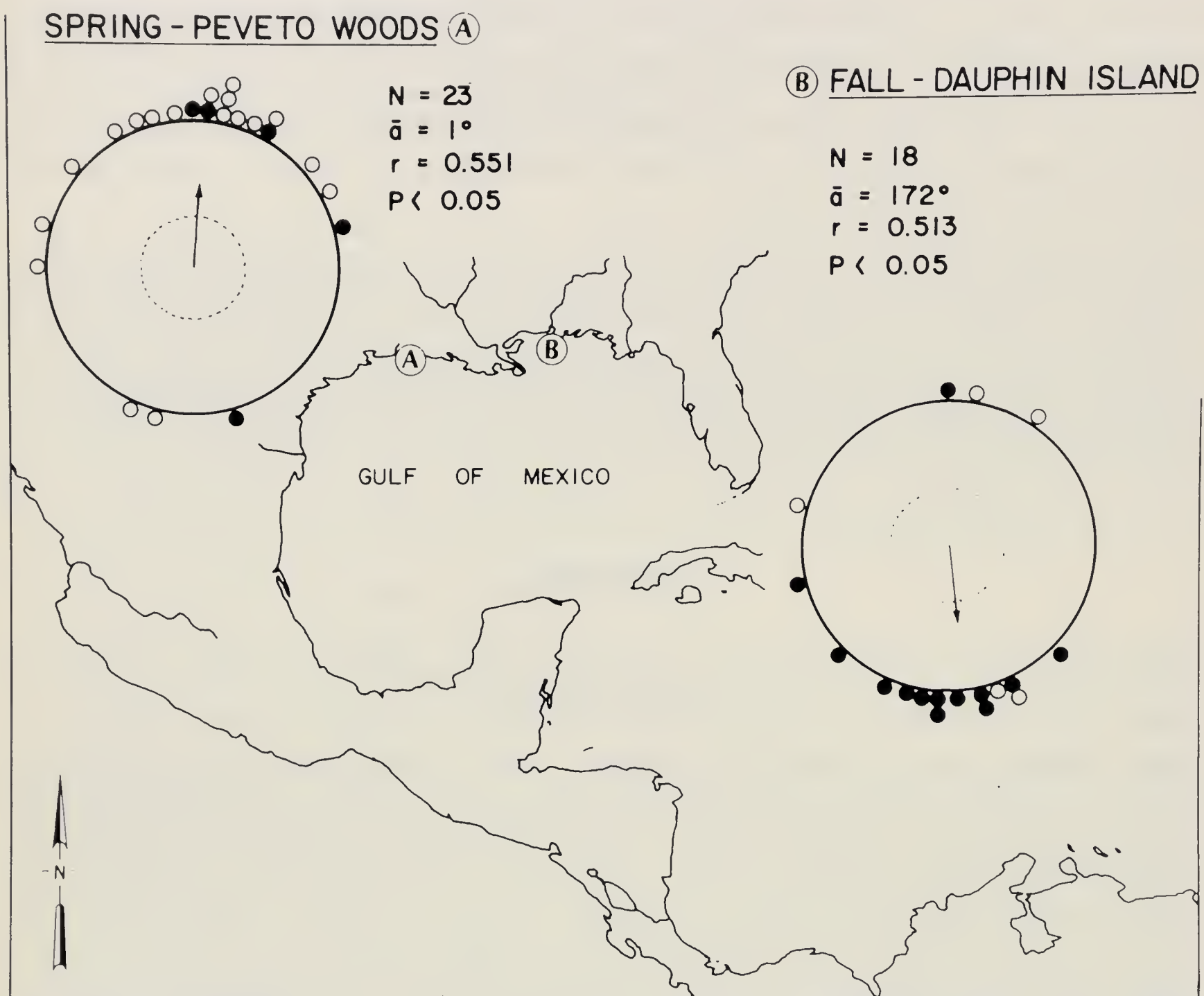


FIGURE 1 - Distribution of nightly headings of Indigo Buntings tested under clear skies in spring at Peveto Woods (left) following trans-Gulf migration and in fall on Dauphin Island (right) before crossing the Gulf of Mexico. The mean vector of the sample is represented by an arrow whose length (r) is drawn relative to the radius of the circle = 1. Open circles represent lean (fat-free) birds and closed circles fat birds.

Anecdotal observations of the departure of landbird migrants from East Ship Island, a barrier island located 19 km off the Mississippi Gulf coast and west of Dauphin Island (Figure 1), before (fall) and after (spring) trans-Gulf migration are consistent with our cage experiment with Indigo Buntings. On several occasions in spring 1988, individuals of several species were observed leaving East Ship Island, either the afternoon of the day migrants arrived on the island or the next morning. On at least three mornings, while travelling by boat from the mainland to the island, passerine migrants were observed flying toward the mainland. Daytime departure from East Ship Island was observed only once in autumn, despite favorable winds and clear indications from day-to-day variation in mist-net samples that birds were leaving the island. On one

morning, several ($N = 12$) landbird migrants departed from the north side of the island and headed toward the mainland.

DISCUSSION

Many landbird migrants make long flights over ecological barriers, and it is obvious that natural selection has favored these flights in spite of the risks and energy demands involved. Migrants should be especially sensitive to the risk of not satisfying energetic requirements when negotiating an ecological barrier. For example, when lean Garden Warblers *Sylvia borin* were placed in activity cages after stopping during trans-Saharan migration, they showed more daytime than night time [migratory] activity (Bairlein 1985). When food-deprived Spotted Flycatchers *Muscicapa striata* and Garden Warblers have been offered food and the opportunity to regain mass, nocturnal (migratory) activity was suppressed, only to resume when mass was regained (Biebach 1985, Gwinner et al. 1985). The amount of stored fat reserve also influenced the decisions of European Robins and Pied Flycatchers *Ficedula hypoleuca* to take off on a migratory flight during free-flight orientation experiments (Sandberg et al. in press).

In our study, lean, essentially fat-free Indigo Buntings which had been captured in fall prior to trans-Gulf migration produced little, if any, nocturnal activity, and when they did, it was just as often oriented north as south. On the other hand, fat-depleted Indigo Buntings that had crossed the Gulf of Mexico in spring were nocturnally active in a seasonally appropriate northward direction (see also Moore 1986, 1990). The behavior of Indigo Buntings is reminiscent of the behavior of European Robins *Erithacus rubecula* in relation to the Baltic Sea in autumn (Sandberg et al. 1988, Karlsson et al. 1988). Birds that had arrived on the southern coast of Sweden (Falsterbo) by overland migration were generally lean and headed north when tested in orientation cages rather than south, which would take them across the Baltic Sea. Their behavior was interpreted as consistent with re-orientation of lean migrants in response to an ecological barrier (Alerstam 1978, Lindstrom & Alerstam 1986). Robins that interrupted their flight over the Baltic Sea to stop at Ottenby along the east coast of Sweden were heavier than Falsterbo birds and oriented their activity in a seasonally appropriate southwesterly direction.

Although Able (1977) found no correlation between the amount of nocturnal activity and fat load while conducting cage orientation experiments with grounded landbird migrants on Block Island (USA) along the Atlantic coast in autumn, he did report a significant relationship between fat load and the likelihood an individual would display *oriented* activity. Moreover, birds of several species oriented their cage activity to the northwest, which was similar to the behavior of free-flying birds during daytime departure from Block Island and consistent with re-orientation in response to an ecological barrier. Others have observed nocturnal migrants re-orienting in flight when they find themselves over the sea at dawn, presumably in response to being offshore (Myres 1964, Richardson 1978). It should come as no surprise that migrants without adequate fat stores either do not attempt long flights over barriers or re-orient away from coastal areas (Alerstam 1990).

Because trying to cross an ecological barrier increases not only energy expenditure but also the possibility a migrant will not meet contingencies that arise, selection

should favor a “margin of safety” in populations of long-distance migrants (cf. Alexander 1981, Lowell 1985). The probability that a certain feature (e.g. fat load or nocturnal timing of migration) will permit an individual to survive reflects both the phenotypic level of the trait and the timing and magnitude of the environmental demands on the trait that the particular individual happens to encounter (e.g. Lima 1986, Rogers 1987). Individuals often bear structures that seem to incorporate more (or less) material or have greater (or lesser) physiological capacity than that needed to let an individual survive at that particular instant in time (Gans 1979). One important cause of excessive capacity is the occurrence of rare events, which nevertheless have important effects on fitness. Such events are likely to have extreme effect on the shaping of phenotype.

Our argument is most easily understood in the context of fat loads, but applies with equal force to other phenotypic traits, including orientation mechanisms (see Sandberg et al. 1988, Alerstam 1990) and the diel timing of migratory flights (see Kerlinger & Moore 1989). Individuals in migratory disposition deposit lipid stores which are mobilized to meet the energetic requirements of migration. Birds not in migratory disposition have lipid contents of only 3-5% of lean body mass whereas intercontinental migrants that cross geographical barriers deposit fat reserves on the average of 30 - 50% of lean body mass (Berthold 1975). The fat reserves of short- and middle-distance migrants average only 13 - 25% (e.g. King & Farner 1965). Landbird migrants typically achieve maximum fat deposition when they reach the point where they must cross a barrier (Gifford & Odum 1965, Marsh 1983) and may not begin to build energy reserves to maximum levels until they encounter the barrier (Odum et al. 1961, Caldwell et al. 1963). Further, migrants apparently deposit excessive amounts of fat in relation to the average maximum demand likely to be encountered while crossing an ecological barrier (e.g. Bairlein 1985, Biebach et al. 1986, Moore & Kerlinger 1987, Safriel & Lavee 1988).

Excess fat deposition represents a “margin of safety” in response to increased variance (unpredictability) associated with long distance flights over ecological barriers. Behavioral and physiological mechanisms mediating fat deposition should be sensitive not only to the average required energy expenditure of such flights, but also to variability in expenditure (*sensu* Alexander 1981, Lowell 1985). We predict that average maximum fat deposition would be greater, relative to the average required level of reserve, for populations of migrants that experience increased variance in realized energetic demand (Figure 2). The behavior of Indigo Buntings before and after crossing the Gulf of Mexico and the behavior of Robins at two sites in relation to crossing the Baltic Sea are consistent with the expectation. Figure 2 illustrates, for a hypothetical “structure”, the average required performance, the average realized performance, and the potential effect of increased variance in maximum load on the margin of safety. The safety factor is the ratio of design strength to the maximum load the structure is expected to have to bear (S/L_{mx}). A higher safety factor is expected in response to increased variance in maximum load (see Lowell 1985). That is, selection should increase the ratio of the performance of a biological structure or system to the requirements placed upon it as conditions become increasingly unpredictable. Increased variance might result from fluctuations in feeding conditions during fat deposition or unpredictable weather over ecological barriers.

Although “strong structures” such as excessive fat or nocturnal migration may be disadvantageous at times (e.g. Lehikoinen 1986, Lima 1986, Martin 1990a), it can be

argued that the selection against the condition represents a balance between the benefit of a modification permitting survival under extreme conditions and the cost of constructing and maintaining such extreme phenotypes at other times (Gans 1974, 1979).

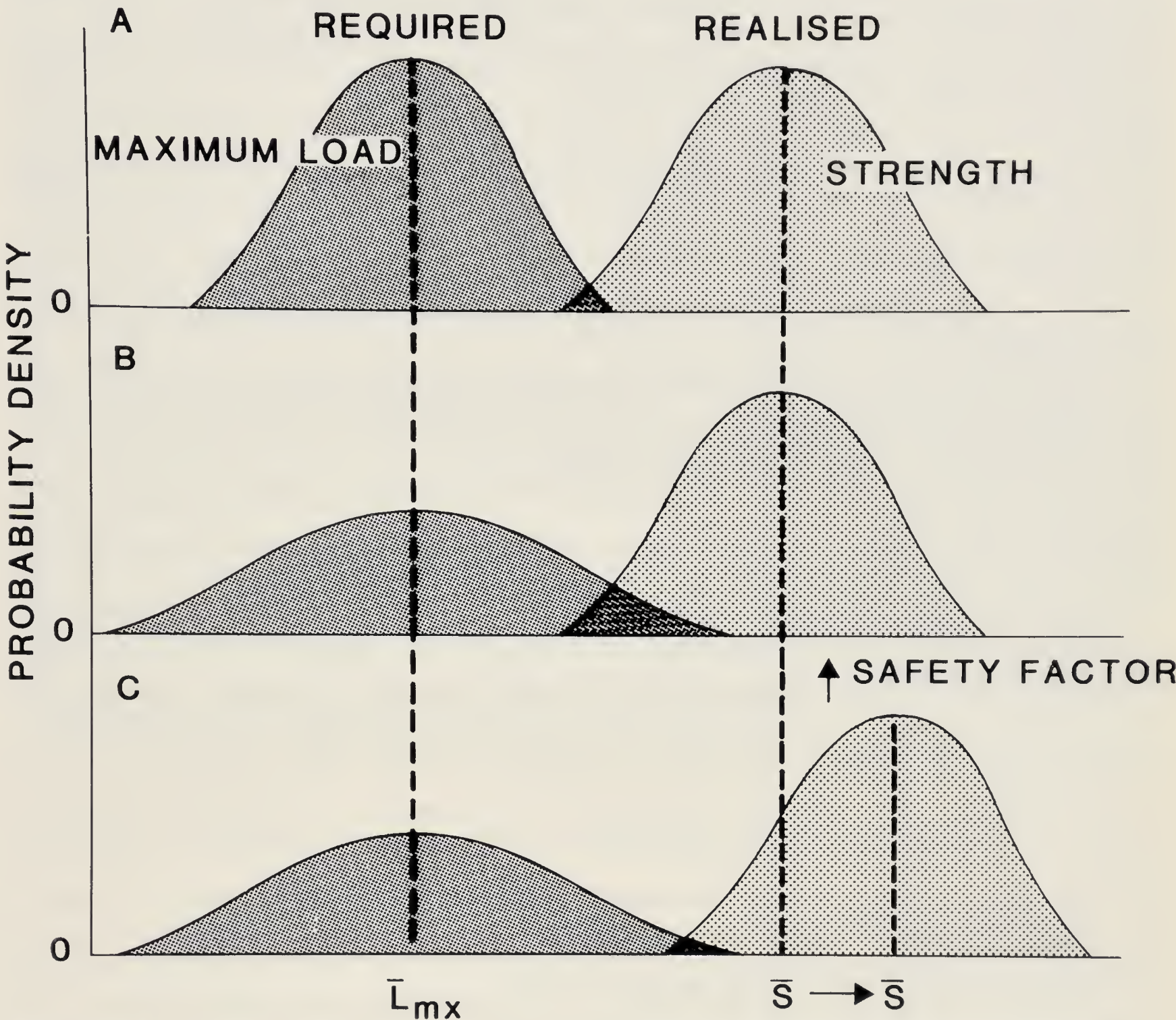


FIGURE 2 - Potential effect of increased unpredictability (variance) in the required maximum fat load on the realized fat load associated with flights across ecological barriers. The curves illustrate the distribution of maximum fat deposits for migrants within a population as variance in required energy demand increased. The diel timing of migration or orientation mechanisms could substitute for fat load. Graphical model adapted from Lowell (1985).

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THE SENSORY BASES OF NOCTURNAL FORAGING IN BIRDS

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ABSTRACT. Audition, olfaction, mechanoreception and taste are the principal senses used in the detection of food items by birds at night. Vision seems to play a secondary role. This is because anatomy and physiology limit the sensitivity and resolution of the avian eye so that it often cannot match up to the visual problems posed by the night environment. Consequently most nocturnal foraging does not involve flight and takes place in open habitats devoid of obstacles. The range of food items taken by nocturnal foragers is restricted to: (1) those which occur at low density but advertise their presence by giving out noise or a strong odour and (2) those which occur at high density and can be detected using touch sensitivity and random searching. Those few nocturnal birds which forage in spatially complex habitats are additionally restricted to a highly sedentary life style.

Keywords: Nocturnality, foraging, senses, vision, hearing, olfaction, mechanoreception, taste, light levels.

INTRODUCTION

This review discusses the sensory bases of foraging in both habitual and occasional nocturnal foragers and uses this information to account for interspecific differences in the propensity to forage at night.

LIMITS ON VISUAL SENSITIVITY

Visual systems are subject to constraints which limit both absolute sensitivity and the amount of spatial information which can be extracted from an image. These constraints arise from the quantal nature of light and from anatomical and physiological constraints on eye structure and nervous systems (Barlow 1981, Snyder et al. 1977).

In strictly nocturnal owls (Strigidae) maximum visual sensitivity and spatial resolution approach these absolute limits. However, these visual capacities are insufficient to cope with all the visual problems posed by night time light levels in the birds' preferred woodland habitats (Martin 1986). Therefore I have argued that nocturnal mobility and prey capture in these owls depends upon the combination of both high visual and auditory sensitivity [auditory sensitivity in owls is close to an ultimate limit imposed by physiological and environmental constraints (Martin 1984)] coupled with a sedentary life style which permits individual birds to gain detailed information on the spatial structure of their home range (Martin 1990).

Outside woodlands light levels are significantly higher (see introduction to this symposium). Any species whose visual sensitivity is near the ultimate limit can detect some visual information under the darkest natural conditions. Even in bright moonlight, however, acuity will always be substantially below that achieved in daylight (Martin 1990).

LIGHT LEVELS AND FORAGING

Despite the assumed primary role of vision in the foraging of many birds, and the large range over which natural light levels can vary (see introduction to this symposium), the influence of light levels on foraging behaviour has received little attention. That foraging efficiency is sensitive to the light level changes of dawn was demonstrated in the Great Tit *Parus major*, a diurnal passerine (Kacelnik 1979). Whether foraging efficiency in nocturnal feeders is similarly sensitive to light level is not known, although Grey Plovers *Pluvialis squatarola* were found to feed more rapidly in moonlight than on moonless nights (Pienkowski 1982). One study followed the foraging success of individual Eurasian Oystercatchers *Haematopus ostralegus* on the same feeding area and recorded that night time feeding rates were about half those of the following day (Goss-Custard & Durell 1987).

Further study of the influence of light levels on nocturnal foraging is clearly worthwhile. However, foraging in some species can occur without the benefit of vision (see below). Thus, foraging owls are willing to fly in complete darkness (Payne & Drury 1958) but these flights are relatively short and occur only in situations familiar to the birds. In nature, visual guidance is still likely to be necessary to guide these birds' flight to foraging areas.

NON-VISUAL CUES AND FORAGING

Field and experimental evidence that foraging birds use non-visual cues is sparse and much of what follows is based upon studies of sense organs rather than of demonstrated sensory capacities.

Audition

Laboratory studies have demonstrated that owls (Strigidae and Tytonidae) can use hearing as the sole cue to prey capture (Payne & Drury 1958, Payne 1971). Owls can locate sounds with a high degree of accuracy; close to that of humans and superior to that of diurnal birds (Knudsen & Konishi 1979, Jenkins & Masterton 1979, Klump et al. 1986). That using only auditory cues to locate prey is part of owls' natural behaviour is suggested by observations of Great Grey Owls *Strix nebulosa* and Short-eared Owls *Asio flammeus* pouncing through a cover of snow or dead grass to snatch mammals from beneath (Hilden & Helo 1981, Clark 1975) and of a Tawny Owl *Strix aluco* catching earthworms by sound cues alone (Macdonald 1976).

Evidence that other nocturnal foragers may employ auditory cues is more circumstantial. Some terrestrial species of shorebirds, particularly the thick-knees *Burhinidae*, forage regularly at night on small vertebrates and large insects, primarily Orthoptera (Cramp & Simmons 1983). The birds usually forage on foot across open terrain. Hald-Mortensen (1970) noted that Stone-curlews *Burhinus oedicephalus* started to forage at dusk at exactly the same time as the Orthoptera started to sing. Fallet (1962) and Lange (1968) proposed that plovers (Charadriidae) may also use sounds when foraging. Here, the cues are made by invertebrates as they move near the mud or soil surface.

Olfaction

Anatomical studies of nasal cavities and olfactory lobes, and some behavioural experiments, attest to the importance of this sense in many bird species (Bang & Wenzel 1985). Some of the most highly developed olfactory apparatus in birds occurs in procellariiforms (Bang 1966), many of which forage at night (Brooke & Prince, this symposium). By day, various procellariiform species (including storm-petrels (Hydrobatidae) and shearwaters (Procellariidae)) were attracted upwind to odours of fish oils, squid and krill, but non-procellariiforms known to be in the area were not attracted (Grubb 1972, Hutchison & Wenzel 1980). At night, storm-petrels, but not shearwaters, were attracted to the pungent bait (Grubb 1972). Jouventin (1977) demonstrated the ability of another procellariiform, the Snow Petrel *Pagodroma nivea*, to detect hidden pieces of raw fish exclusively on the basis of olfactory cues. Thus, there is good evidence that procellariiform seabirds can use olfactory cues to guide them to food sources. Whether the use of such cues is sufficient to account for all nocturnal foraging in these birds is not certain.

The role of olfactory cues in the foraging of kiwis (Apterygidae) has been demonstrated by the birds' ability to detect hidden earthworms (Wenzel 1968). The olfactory apparatus of kiwis is particularly large (Bang 1971) and there seems little doubt that olfaction plays a key role in the nocturnal behaviour of these flightless birds (Reid & Williams 1975).

Olfaction has also been ascribed an important role in the foraging of the frugivorous, nocturnal Oilbird *Steatornis caripensis*, whose olfactory apparatus is among the most elaborate of any species (Bang & Wenzel 1985). However, olfactory prowess has not been investigated. When foraging the birds usually fly above rather than below the tree canopy. Since the sought-for fruits occur in tree tops bunches the birds may locate them by their odour, the bunch acting as an olfactory beacon, and/or in silhouette against the sky (Snow 1961). Oilbirds can echo-locate but this does not yield fine spatial detail and is rarely used outside caves (Konishi & Knudsen 1979).

Mechanoreception

Touch sensitivity both within and on the surface of the bill serves an important role in the feeding behaviour of many birds (for review see Gottschaldt 1985). It plays a particularly significant role in waterfowl and shorebirds and it seems that this enables species in these taxa to extend their foraging, either regularly or occasionally, into the night.

Among shorebirds the degree of dependence upon touch sensitivity in detecting invertebrate prey items is probably related to bill length. The number of tactile receptors around the tip of the upper mandible is greater in longer-billed species (Bolze 1968). Species with shorter bills, such as plovers (Charadriidae), are thought to be guided primarily by hearing (see above) and/or vision (Pienkowski 1982) to prey. These species are less likely to feed at night or may do so principally under moonlight (see McNeil this symposium).

Longer-billed species use a variety of probing actions to locate prey buried in soft substrates (Cramp & Simmons 1983) and they are probably guided exclusively by tactile receptors at the bill tip (Gottschaldt 1985). Some species, such as Eurasian Curlews *Numenius arquata*, can locate, identify and ingest food items without

removing the bill from the substrate (Hale 1980). Thus these longer-billed shorebirds can forage entirely without the aid of visual cues.

Waterfowl can similarly forage without the aid of visual cues. The upper mandible in these species is equipped with a "bill tip organ". This is regarded as one of the most sophisticated sensory structures occurring in vertebrate skin (Gottschaldt 1985). That waterfowl can use this organ as the sole means of locating food items was demonstrated in Mallard Ducks *Anas platyrhynchos*, which discriminated between peas and dummy items buried in wet sand and ingested the food without bringing the bill above the surface (Zweers & Wouterlood 1973).

There is a clear need for further investigation of the role of bill tip organs in foraging. Especially interesting is the possible role of this organ in the feeding of diving ducks, many of which feed at night (Owen, this symposium).

Evidence that other species employ touch sensitivity as the principal basis for locating food at night is less direct. Thus nightjars (Caprimulgidae) take insects of a large size range, mainly from the airspace above vegetation. The palate of these birds has an apparently unique, highly vascularised membrane which is thought to be touch sensitive. It could act to trigger the closing of the bird's wide gape when an insect enters the mouth during open-billed trawling (Cowles 1967). Rictal bristles surround the upper mandible of nightjars and these could function to guide insects towards the open mouth and/or function as tactile receptors to guide the mouth towards prey. The possible sensory function of rictal bristles has not, however, been studied.

Touch sensitivity in the lower mandible could be the key means by which skimmers (Rynchopidae; Charadriiformes) detect food items. These birds often feed at dusk and at night on calm open water, flying with the uniquely elongated lower mandible trailing just below the water surface (Zusi 1962). However, fish are not simply scooped from the water in random searches. Sensory signals from the lower mandible must play a role since fish are caught when the bill closes rapidly immediately a prey item touches the trailing mandible (Zusi 1962).

Blind-folded Wood Storks *Mycteria americana* can catch live fish as quickly as when sighted, presumably by virtue of tactile cues from the bill (Kahl & Peacock 1963). Thus, the possible role of touch sensitivity in the bill of occasional night foragers among the herons (Ardeidae) and storks (Ciconiidae) would be worth investigating.

Taste

The primary function of taste reception is to screen food and water intake by analysis of its chemical composition (Berkhoudt 1985). There is evidence that taste can also guide foraging behaviour and this may be important in some nocturnal foragers. Thus, Van Heezik et al. (1983) and Gerritsen et al. (1983) demonstrated that four species of *Calidris* shorebirds could discriminate between jars filled with sand containing "taste" and "no-taste". Taste came from worms which had been removed from the jars. No-taste was simply the washed sand. The birds probed in the taste sand for a significantly greater proportion of the foraging period than in the visually identical no-taste sand. Thus shorebirds, whether feeding by day or night, could choose which patch of a uniform substrate to probe on the basis of chemical signatures left behind by favoured prey.

CONCLUDING REMARKS

This review is not a comprehensive account of the sensory bases of nocturnal foraging in birds. Many nocturnal foragers have not been mentioned because there are no specific clues on the sensory bases of their foraging. Much could be conjectured. For example, hearing may play an important role in the foraging of frogmouths (Podargidae) and in some night foraging herons (Ardeidae), but there is no specific evidence on this. However, some themes which may have general applicability can be discerned from the evidence presented.

- (1) In view of the constraints on visual performance in relation to night-time light levels, it is understandable that few of the regular, and none of the occasional, nocturnal foragers make use of spatially complex habitats, such as forests. Most nocturnal foraging takes place in open habitats, often associated with water or in the air space above vegetation.
- (2) When nocturnal foraging does occur beneath a closed woodland canopy, as in some of the owls, sensory limitations require the birds to have a particularly sedentary life style. This enables the birds to become familiar with the structural complexity of their home range and permit activity guided only by limited sensory information.
- (3) While vision cannot be dismissed as unimportant in guiding the flight and nocturnal foraging behaviour of birds, in no species does it seem sufficient to account for the ability to forage at night. Thus, food items taken by nocturnal foragers tend to be restricted to two main types which can be detected by non-visual cues: (i) Items which may occur at low density but advertise their presence by giving out a strong odour (e.g. ripe fruits, Oilbird; fish, cephalopods and crustaceans, procellariiforms; soil invertebrates, kiwis) or produce sounds either intrinsically or as they move (e.g. small mammals, owls; large insects, terrestrial shorebirds; invertebrates of mud or soil, shorebirds); (ii) Items which occur at high density and can be detected using touch sensitivity and random searching (e.g. short vegetation, seeds and surface invertebrates, waterfowl; aerial insects, nightjars; surface and buried invertebrates, shorebirds; surface fish and invertebrates, skimmers).

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SYMPOSIUM 18

**SOCIAL ORGANISATION OF NECTAR-FEEDING
BIRDS**

Conveners B. G. COLLINS and F. L. CARPENTER

SYMPOSIUM 18

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INTRODUCTORY REMARKS: SOCIAL ORGANIZATION OF NECTAR-FEEDING BIRDS

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Nectarivorous birds are abundant in many parts of the world. The most prominent of these are the honeyeaters (Meliphagidae) of Australasia, sunbirds (Nectariniidae) and sugarbirds (Promeropidae) of Africa, white-eyes (Zosteropidae) of Asia and Oceania, and hummingbirds (Trochilidae) of northern and neotropical America (Landsborough-Thompson 1964, Maclean 1985, Collins & Paton 1989).

Many nectarivores appear to be quite flexible in their diets, making use of materials such as nectar, arthropods, fruit, manna, honeydew and lerp (Pyke 1980). Honeyeaters, in particular, have an obvious capacity to vary the proportions of various food items ingested from one location to another, and from season to season (Pyke 1980, Collins et al. 1990). All items consumed presumably have some nutritional value, although nectar usually appears to be the major source of energy for these birds (Hainsworth & Wolf 1976, Collins & Paton 1989).

Nectarivorous bird communities in many parts of North America and Africa are relatively simple, often comprising only one or two types of bird that forage for nectar at any given time (Paton & Carpenter 1984). Community organization is considerably more complex in the neotropics, and in most Australian habitats, where the numbers of competing nectarivores and potential nectar sources are much greater (Feinsinger 1976, Collins & Newland 1986). Within such habitats, spatial and temporal variations in the distribution of nectar resources can be considerable (Collins & Grey 1989, Collins et al. 1990). Nectarivores are thus presented with a diversity of foraging options.

The social status of species and individuals and the ability of these birds to harvest nectar and other nutrients are influenced by several factors. Included among these are morphological characteristics such as body mass and wing disc loading, and other parameters such as environmental temperature and activity patterns that influence the energy requirements of these birds (Collins & Paton 1989). Dominance hierarchies are often established, with larger, more aggressive birds sometimes defending territories that contain the richest and most profitable sources of nectar. Subordinate birds are sometimes opportunistic, although often obliged to use widely dispersed and low-reward sources of food.

The five papers presented in this symposium deal with various aspects of social organization and nectar use within nectarivore communities. McFarland & Ford discuss relationships between honeyeater foraging and social behaviour in Eastern Australia, Carpenter et al. describe sexual differences in the acquisition of nectar by migrant Rufous Hummingbirds, and Collins & McNee provide an energetic explanation for the

partitioning of nectar resources within honeyeater communities in Western Australia. Tiebout outlines the energetics of competition within neotropical hummingbird communities, and Rebelo discusses the social organization of nectarivorous birds in southern Africa. The symposium concludes with Carpenter providing a brief synthesis of ideas raised and making suggestions as to appropriate future research.

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THE RELATIONSHIP BETWEEN FORAGING ECOLOGY AND SOCIAL BEHAVIOUR IN AUSTRALIAN HONEYEATERS

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ABSTRACT. The Australian honeyeaters (Meliphagidae) are a diverse and successful family, occurring in all types of habitat. They also show a wide range of food, feeding behaviour and social and breeding behaviour. Over the last two decades, there have been several studies on honeyeater communities and on individual species. Honeyeaters can be loosely separated into two guilds. Members of the first are dependent on nectar for most of the year, whereas those in the latter are more insectivorous. Alternative carbohydrate sources such as honeydew, lerp and manna are exploited by both groups. Several species also consume fruit. Nectarivorous species range from solitary and territorial to loosely social. The New Holland Honeyeater *Phylidonyris novaehollandiae* has been well studied and is strongly territorial at moderate densities of nectar. Juveniles may remain within parental territories for some months after independence. Neighbouring pairs may co-operate in mobbing predators near nests. In the larger wattlebirds (*Anthochaera*) and friarbirds (*Philemon*), breeding and feeding territories may be held, but sometimes flocks congregate at flowering trees. The insectivorous honeyeaters range from strictly pair-territorial (e.g. Yellow-faced Honeyeater *Lichenostomus chrysops*), through semi-colonial and partly cooperative (e.g. Fuscous Honeyeater *L. fuscus*) to species with highly complex cooperative breeding systems (e.g. Noisy Miner *Manorina melanocephala*). The latter dominate locally rich sources of food and have a major impact on the bird community. An understanding of honeyeater biology at the specific and community level illustrates the importance of conserving areas with a spectrum of rich through to poor resources, if the aim is to retain a diversity of bird species.

Keywords: Foraging ecology, social behaviour, honeyeaters, Australia, nectar, cooperative breeding, diversity.

INTRODUCTION

In this paper we investigate relationships between honeyeater feeding and social behaviour (Table 1). Comprising between 160 and 170 species, the Meliphagidae form a diverse passerine family distributed throughout the Australasian region with a few Oriental species. Most species are in Australia (64-68 spp.) and New Guinea (65 spp.) (Blakers et al. 1984, Beehler et al. 1986). Australian species occupy a wide range of habitats, including tropical rainforest, montane forest, woodlands, heathlands and mangroves, as well as mallee and arid shrublands (Schodde & Tidemann 1986).

GUILDS AND FOOD RESOURCES

Honeyeaters can be loosely separated into two guilds based on beak length (Ford 1979). Long-billed species are dependent on nectar for most of the year. Nectarivorous honeyeaters visit a wide variety of plants, mostly of the families Proteaceae, Myrtaceae and Epacridaceae (Paton 1986) and range considerably in body size from the Scarlet Honeyeater (8 g) to the Yellow Wattlebird (150 g). They also take insects often by hawking. Short-billed species are more insectivorous, taking arthropods from foliage, bark and in flight, and span a smaller body size range (e.g. Dusky Honeyeater c.13 g to Noisy Miner c.60 g).

TABLE 1 – Features of honeyeater foraging ecology and social behaviour referred to in this paper.

Foraging ecology	Social behaviour
<i>Habitat</i>	<i>Mobility</i>
<div><div>- forest, woodlands, heathlands</div><div>- distribution and abundance of food</div></div>	<div><div>- sedentary, locally nomadic, long distance nomad or migrant</div></div>
<i>Food types</i>	<i>Spacing behaviour</i>
<div><div>- proportions of nectar, insects, fruit and alternative carbohydrates in diet</div></div>	<div><div>- breeding and non-breeding season</div><div>- solitary, territorial, colonial, flocking</div></div>
<i>Foraging behaviour</i>	<i>Mating system</i>
<div><div>- method: hawking, gleaning</div><div>- substrates and plants used</div><div>- height in vegetation</div></div>	<div><div>- monogamous, polygamous</div></div>
	<i>Parental care</i>
	<div><div>- pair, co-operative</div></div>

While the timing of flowering may be seasonally predictable, the productivity and spatial distribution (local and regional scales) of the nectar supply can vary within and between years (Pyke 1983, 1985, Collins & Newland 1986), and even over successive days (McFarland 1986a). Insects generally show less seasonal fluctuation in abundance in any locality (Woinarski & Cullen 1984, Bell 1985), but their abundance can be quite spatially variable, particularly as a result of the distribution of certain plant types and the effects of localised infestations (Wykes 1985, Dunkerley 1989). Honeyeaters mostly take small insects, which vary less seasonally than large insects. The distinction between the two honeyeater guilds is loose because some species, especially insectivorous ones, may exhibit seasonal, local and opportunistic differences in diet (Paton 1980, Wykes 1985, Ford 1989, Reid 1990).

Paton (1980) found that ‘insect feeding’ by honeyeaters from both guilds also included alternative carbohydrates. These sugary substances occur as plant exudates (manna) and the covers (lerps) or secretions (honeydew) of sapsucking nymphs, such as psyllids and scale insects. They resemble nectar in having a high energy content, and are renewable resources, but are collected using methods typical of insect foraging, i.e. foliage gleaning and bark probing (Woinarski et al. 1989). All three food types are widely distributed and found on most species of *Eucalyptus*. More numerous than foliage or bark insects, the carbohydrates are available seasonally (manna, honeydew) or year round (lerp, honeydew) (Paton 1980).

Honeyeaters of both guilds are highly flexible and overlap extensively in most other aspects of foraging, e.g. substrate type, plant type and height in vegetation (Keast 1985, Recher & Holmes 1985, Ford et al. 1986). Consequently, attributes of foraging ecology will not be considered further when discussing social behaviour.

Fruit is also eaten by some honeyeaters. In rainforests, tropical and arid habitats, fruits are available all year (Forde 1986, Reid 1990) or seasonally with only a short period of scarcity in spring (Crome 1975, Innis 1989), so frugivorous honeyeaters are found mostly in these habitats (Table 2).

TABLE 2 – Percentage of honeyeater species in different habitats taking different food types (n = number of species; habitat preference from Blakers et al. 1984; food preference from Schodde & Tidemann 1986). ^a includes lerp, honeydew and manna; ^b includes mangroves; ^c includes paperbark swamps and mallee; ^d includes very open woodland; ^e Tr = Tropical, Te = Temperate.

Food type	Rainforest		Open forest ^b		Woodland ^c		Heath Arid/Semi-arid ^d shrubland	
	Tr	Te ^e	Tr	Te	Tr	Te		
Nectar	12	50	47	41	35	41	88	33
Insect ^a	44	-	47	53	50	50	12	45
Fruit	44	50	6	6	15	9	-	22
n	9	2	15	17	26	32	8	9

TABLE 3 – Percentage of honeyeater species in various mobility categories that take different food types (n = number of species; data from Schodde & Tidemann 1986; many species were counted in two or more categories). ^a has same meaning as in Table 2.

Food type	n	Mobility category		
		Sedentary	Locally nomadic	Highly nomadic/Migratory
Nectar	58	31	41	28
Insect ^a	55	49	38	13
Fruit	15	53	40	7

A FAMILY OVERVIEW

Nectarivorous species are proportionally most common in heathlands and tropical forests (Table 2). Heathlands and forests with heathy understoreys have flowers present for most of the year, but are comparatively depauperate in insects (Pyke 1983). Bird communities in these habitats are usually dominated by honeyeaters (10+ species), with one or two other nectarivorous birds such as lorikeets (Loriidae) and/or silvereyes (Zosteropidae) (Ford 1989). All of these birds generally perch and probe into flowers to obtain nectar.

Honeyeaters that collect insects and alternative carbohydrates are common in all habitats except heathlands (Table 2). Most insectivorous species occupy specific habitats, and consequently there are rarely more than 3-5 syntopic species (Ford & Paton 1976, 1977, Wykes 1985).

Species from both honeyeater guilds range from sedentary to locally nomadic and long distance nomads or migrants (Table 3). While most of the sedentary species are

insectivorous, nectarivorous birds form the greatest proportion of locally and highly nomadic groups. This can be explained by the differences in the temporal and spatial patchiness of the different food resources, with nectar-feeders generally having to travel more widely in search of nectar (Keast 1976).

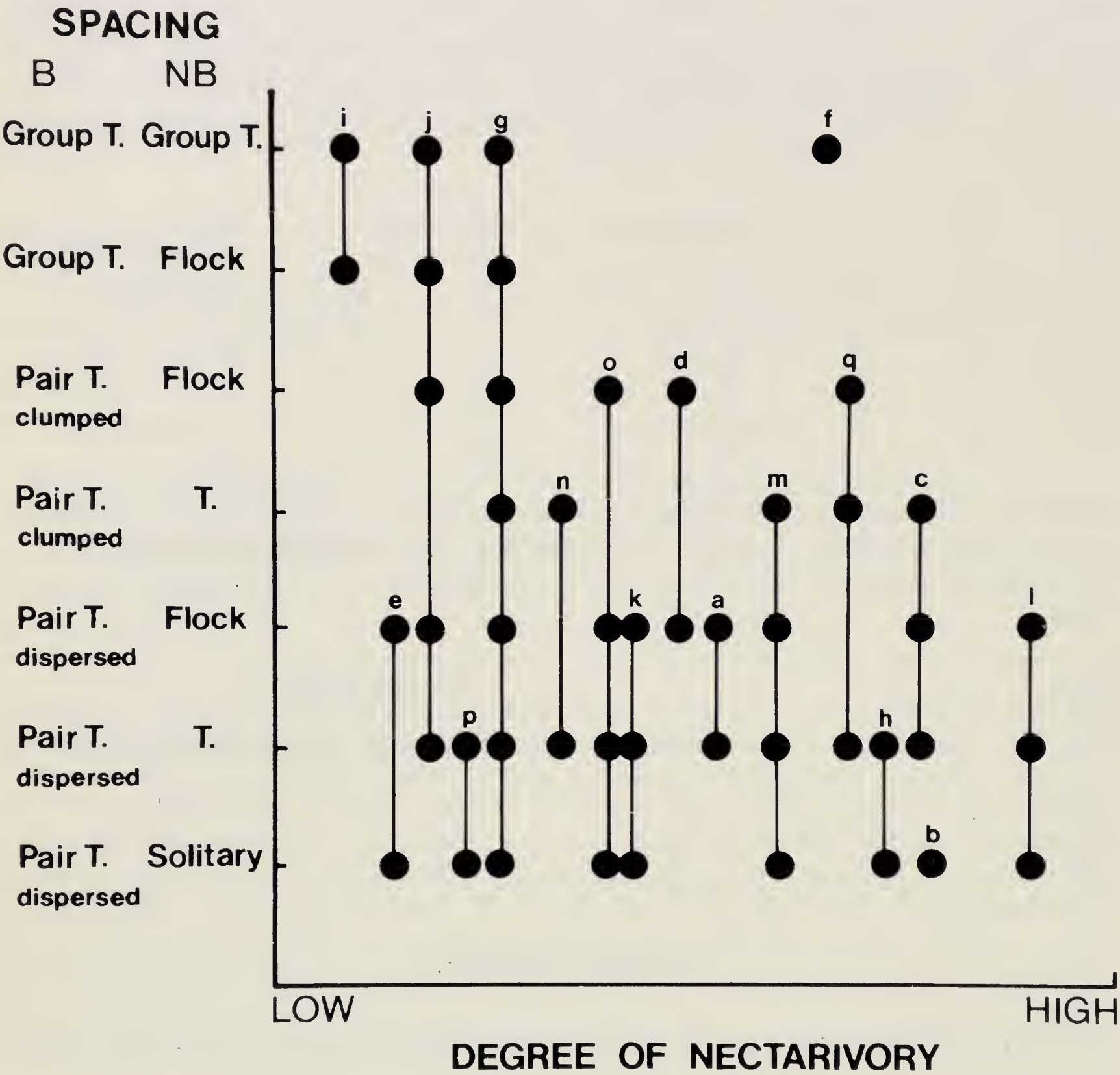


FIGURE 1 – Distribution of Australian honeyeaters in terms of the degree of nectarivory and their spacing systems during the non-breeding and breeding seasons. Frugivorous species have been omitted. Data from Schodde & Tidemann 1986. Genera denoted by: a. *Acanthagenys*; b. *Acanthorhynchus*; c. *Anthochaera*; d. *Certhionyx*; e. *Conopophila*; f. *Entomyzon*; g. *Lichenostomus*; h. *Lichmera*; i. *Manorina*; j. *Melithreptus*; k. *Myzomela*; l. *Philemon*; m. *Phylidonyris*; n. *Plectorhyncha*; o. *Ramsayornis*; p. *Trichodere*; q. *Xanthomyza*.

Honeyeaters exhibit many different spacing systems (Figure 1). Even though we recognise the flexibility in breeding and non-breeding social behaviour of honeyeaters, we will use standard spacing terminology for the sake of convenience. The categories used are: territorial (defence of area/resources by individuals, pairs or groups; territories may be clumped as colonies or dispersed); solitary (individuals alone but may form unstructured aggregations at food resources); and flocks (groups of birds moving together as identifiable units). Species may shift between different systems

during the year or may exhibit one social behaviour at all times. Individual honeyeater genera can span several systems, with insectivorous ones showing a greater diversity than nectarivorous honeyeaters (Figure 1).

The pattern in Figure 1 could be due to differences in the predictability of food resources. Nectar, while it can be highly profitable energetically, often attracting numerous species into an area (Ford 1979, Paton 1979, McFarland 1986a), is a more variable resource than insects. Many of the nectarivorous honeyeaters (*Anthochaera*, *Philemon*, *Acanthorhynchus*) must therefore be continually on the move in search of flowers (Table 3). The short-term availability and rapid depletion of nectar may favour territorial or solitary behaviours that enable birds to gain 'short-term' access to transient or patchy nectar resources (Ford 1981, McFarland 1983). Insectivorous species, faced with a more consistent but spatially variable resource, are more sedentary but often defend rich patches as groups on either a continuous or seasonal basis. The nature of these groups, e.g. *Manorina* spp., may be highly complex and co-operative (Swainson 1970, Dow 1978, 1979a, b), or loosely colonial, as is the case with some *Lichenostomus* spp. (Immelmann 1961, Dunkerley 1989). Less social insectivores may hold interstitial breeding territories or form flocks in the non-breeding season (Wykes 1985).

TABLE 4 – Number of honeyeater species in nectarivorous and insectivorous guilds for which there are observations of possible co-operative breeding activity (Definite = > 2 individuals seen feeding young, Suspected = > 2 birds seen near or at nest). Data from Dow 1980, Moffatt et al. 1983, Ford et al. 1988 and Schodde & Tidemann 1986.

Honeyeater guild	Genera	Number of species		
		In genus	Definite	Suspected
Nectarivorous	<i>Anthochaera</i>	4	-	1
	<i>Entomyzon</i>	1	-	1
	<i>Philemon</i>	4	-	1
	<i>Phylidonyris</i>	5	-	1
	TOTAL	14	0	4
Insectivorous	<i>Conopophila</i>	3	1	-
	<i>Lichenostomus</i>	18	2	4
	<i>Manorina</i>	4	3	1
	<i>Melithreptus</i>	6	3	3
	<i>Plectorhyncha</i>	1	1	-
	TOTAL	32	10	8

Australian honeyeaters are monogamous, with the only known exception being the promiscuous Noisy Miner (Dow 1978). Parental care ranges from only the pair being involved (female ± male engage in nest building and incubation, both feed young) to the presence of helpers (co-operative feeding of young). Of the 22 Australian honeyeater species for which there are indications of co-operative breeding, 18 are in the insectivorous guild and only 4 in the nectarivorous group (Table 4). This is consistent with the findings of Ford et al. (1988), who demonstrated that nearly all co-operative breeders in Australia are insectivorous. These workers also suggested that the highest concentrations of co-operative species occur in areas with the lowest seasonality of food resources. The variability of nectar in both time and space may

account for the low incidence of confirmed co-operative breeding among nectarivorous honeyeaters. Nectar-feeding birds may be unable to 'share' effectively a widely fluctuating resource. Also, their mobile nature would make group cohesion difficult.

INTERSPECIFIC COMPARISONS

Nectarivorous guild

Wattlebirds *Anthochaera* spp. and friarbirds *Philemon* spp. are very mobile and in some instances migratory (Keast 1968, Blakers et al. 1984). In the non-breeding season they may move about singly and quietly defend individual feeding territories (Paton 1979, Ford 1981, Armstrong unpubl. data) or flock around nectar sources, from which they may attempt to exclude other nectar-feeding birds (Hindwood 1944, Bruce 1973, McFarland 1985). Because they are large, wattlebirds and friarbirds are often able to dominate aggressively other honeyeater species when aggregating at rich flower sources (Magarry 1983, McFarland 1986a). Wattlebird and friarbird breeding pairs are generally well-spaced (Hindwood 1944, but see Hindwood & McGill 1951), and territories do not necessarily include rich nectar patches (Ford unpubl. data). Indeed, wattlebirds may be chiefly insectivorous while breeding.

Non-breeding spinebills *Acanthorhynchus* spp. can be nomadic on local and regional scales (Blakers et al. 1984) and may occur as high-density aggregations at flowering trees or shrubs (McFarland & Ford 1987). Feeding territoriality has not been recorded, but Eastern Spinebills will use intraspecific threat displays to gain short-term access to *Banksia* flowers (McFarland 1983). Spinebills tend to be low in the interspecific dominance hierarchies and may be excluded from nectar-rich areas (Ford & Paton 1982). When breeding, spinebills are territorial with the pair defending the nest and adjacent flowers (White 1940, Immelmann 1960).

The New Holland Honeyeater is the best studied nectarivorous honeyeater. It exhibits a number of different social systems, and will be discussed in detail later.

Insectivorous guild

White-eared Honeyeaters are specialised bark foragers (Ford & Paton 1976), with sedentary pairs occupying non-contiguous all-purpose territories (Figure 2, Recher & Abbott 1970, Wykes 1985). Yellow-faced Honeyeaters also breed in dispersed pair territories, from which they migrate, often returning to the same territory in subsequent years (Bell & Ford 1987) (Figure 2). These flocks may migrate considerable distances (Keast 1968) and generally feed at undefended resources, though as flocks they can swamp the territories of larger and more aggressive species (Wykes 1985). The territories of both White-eared and Yellow-faced Honeyeaters are usually situated in areas not occupied by the more dominant, group-forming honeyeaters.

The Fuscous Honeyeater is a generalised feeder, taking various foods by several methods on most substrates at most heights (Ford et al. 1986). This species aggressively dominates smaller insectivores, including other honeyeaters (e.g. *Melithreptus*) within its preferred habitat – eucalypt woodland (Dunkerley 1989). When not breeding, individuals or small groups may wander locally, establishing short-term feeding territories on temporarily rich foods (e.g. insect outbreaks), or parts of the population may migrate (Figure 2, Wykes 1985, Dunkerley 1989).

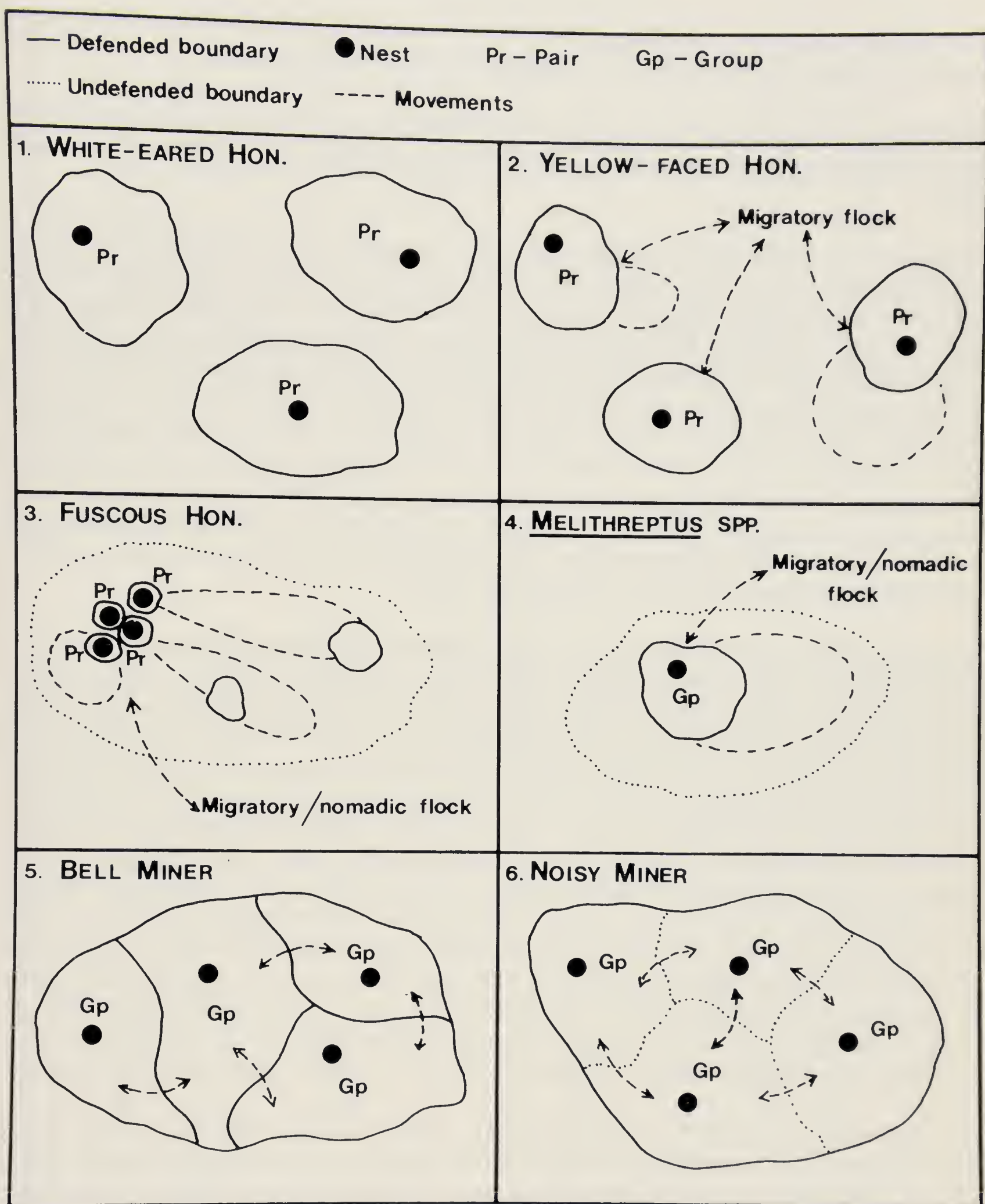


FIGURE 2 – Schematic representation of the spacing systems displayed by insectivorous honeyeaters. Nectarivorous honeyeaters usually have systems similar to either 2 or 3. All systems are characterised by individual dispersers and so these have not been shown.

Fuscous Honeyeaters are monogamous, with no reports of helpers at the nest. However, adjacent pairs will engage in corroborees (group displays) and co-operate in mobbing intruders. Nests are often clumped and most foraging is done away from the nest site. Dunkerley (1989) noted that nests with close neighbours were nearly three times more likely to succeed than isolated nests. She suggested that access to food resources is sacrificed for increased detection and more effective mobbing, and re-

removal of predators and intruding competitors. Absence of competitors may also improve the foraging efficiency of the resident Fuscous Honeyeaters.

Melithreptus honeyeaters live in family groups which are not strongly aggressive and which may move locally or migrate (Figure 2, Noske 1983, Schodde & Tidemann 1986).

Bell Miners live in colonies of largely sedentary family groups consisting of a monogamous pair and several helpers (Clarke 1988). The Bell Miner feeds mainly on lerps, and colonies are sited in areas with a rich and reliable source of psyllids. Colonies will shift into and monopolise areas where and when an infestation occurs (Wykes 1985). Each family group in the colony has an all-purpose territory (Figure 2) which is defended against all species, especially potential competitors (Swainson 1970, Smith & Robertson 1978). Miners, by their interspecific aggression and use of harvesting strategies, are able to improve the spatial and temporal predictability of lerps, thereby maintaining a rich and reliable food source (Loyn et al. 1983). Cooperation occurs both within and between groups, with helpers feeding the young of other families as well as their own. Individuals will also cross boundaries to assist in chasing intruders and mobbing predators (Smith & Robertson 1978).

The Noisy Miner is at the pinnacle of complexity in honeyeater social behaviour (Dow 1977, 1978, 1979a, b). This colonial species is a foliage and ground gleaner, taking insects and alternative carbohydrates, as well as nectar when available. Exclusive access to nearly all food in an area is gained through indiscriminate interspecific aggression (Dow 1977). Honeyeater and non-honeyeater species are attacked and individuals of smaller species may be killed. Intraspecific aggression is common within a colony, which is not unexpected since a colony may comprise several hundred birds. However, all members will co-operate to mob predators and expel intruders. Noisy Miners are also co-operative breeders. In the sedentary colony, groups of males, which outnumber females 3:1, occupy certain areas, but individuals can move between groups (Figure 2). Females avoid each other, have restricted ranges, and when nesting become the focus of attention of the males. Mating is promiscuous and, while the females alone build the nests and incubate the eggs, feeding the chicks and fledglings is undertaken by the males. On average, 12 males attend a nest and a single male may be visiting up to four different nests in the colony (Dow 1978, 1979a, b).

The low seasonal variation, but patchiness, of some insect resources in eucalypt woodlands may be important in the evolution of complex social systems among insectivorous honeyeaters. In turn, the level of group cohesion (ranging from a loose pair aggregation to a fully co-operative colony) may be vital in determining access and degree of exclusive use of food resources in an area. Those with highly developed behaviour monopolise rich areas, even aggressively excluding larger species, while simple pair species use interstitial patches of usually poorer resources (Wykes 1985, Dunkerley 1989). However, the latter honeyeaters may gain temporary access to better sites by forming flocks and swamping the territories of other species.

INTRASPECIFIC COMPARISONS

The well-studied, nectarivorous New Holland Honeyeater displays a diversity of social behaviours that may depend on the distribution and relative availability of nectar.

TABLE 5 – Summary of the social systems of the New Holland Honeyeater; ^a denotes availability of nectar required to meet honeyeater needs over most of study period; ^b density of New Holland Honeyeaters (birds/ha); N.D. no data available.

Study	Habitat	Study period	Nectar availability ^a	Distrib.	NHH ^b	Spacing system	
						Non-breed.	Breeding
1. Pyke (1983,1985)	Heathland	All year	Non-limiting	Dispersed	4.7	Transient, non-territ.	N.D.
2. Recher (1977), Carpenter (1978)	Heathland	All year April-June	Very abundant	Dispersed	5.9	Non-territ. aggrega-	Nest-site territ.
3. Bell (1966)	Heathland	All year	Very abundant	Dispersed	3.0	Non-territ.	Nest-site territ.
4. McFarland & Sale (1986)	Heathland	Feb - Aug	Non-limiting	Dispersed	3.9	Non-territ.	Nest-site territ.
5. Armstong (unpub. data)	Heathland	All year	Sometimes limiting	Dispersed	N.D.	Non-territ.	Territ.
6. Ford & Paton (1982)	Forest/heathland	May - June	Limiting	Dispersed	10.0	Feeding territ.	N.D.
7. Paton (1979)	Forest	All year	Limiting	Dispersed	12.5	Feeding territ.	Food + nest territ.
8. McFarland (1985, 1986a,b,c)	Forest	All year	Limiting	Dispersed	4.9	Feeding territ.	Nest + food territ.
9. Rooke (1979)	Forest	All year	N.D.	Clumped	16.0	Dominance hierarchies	

When nectar is abundant (Table 5), New Holland Honeyeaters are non-territorial outside the breeding season, often moving locally in loose family groups (Recher 1977). During breeding, which may last 8-10 months each year, only the nest site and a small surrounding area are defended. However, Armstrong (unpubl. data) has found that small defended areas (c.30 m radius) have unclear boundaries and are not centred on either nectar resources or nests. Aggression does not appear to be correlated closely with nectar availability, as nectar supplementation during these periods did not alter the seasonal patterns. Armstrong suggested that the honeyeaters are most aggressive when they are establishing territories.

Where nectar was depleted daily or localised for much of the year, New Holland Honeyeaters maintained some form of dominance over larger areas (Table 5). In Victoria, Paton (1979, 1985) described birds defending economical feeding territories based on a variety of plant species, as well as on honeydew and manna. Smaller and similar-sized honeyeaters were aggressively excluded, using both energetically inexpensive (e.g. displacement) and expensive (e.g. chase) methods, depending on the costs and benefits of the defended resource. However, flocks of intruders sometimes swamped territories. Larger intruders, e.g. Red Wattlebirds, were harassed by owners using 'flitting' displays in an attempt to reduce the intruders' foraging efficiency.

A similar situation was found in a montane population in New England (Table 5, McFarland 1985, 1986 a,b,c), though there were some significant differences. In New England, the nectar supply varied from day to day due to weather, and feeding territories economically defensible one day were uneconomical the next. Faced with varying nectar levels, owners adjusted their foraging time and, rather than alter boundaries or abandon the site, modified their aggression and degree of territory exclusiveness. Time spent in aggression was highest at moderate nectar levels ($0.5 \text{ kJ/m}^2 = 1.9\%$) and lower when nectar was either scarce or super-abundant ($0.05 \text{ kJ/m}^2 = 1.3\%$, $3.0 \text{ kJ/m}^2 = 0.8\%$, McFarland 1986a). Paton (1979) noted that nectar levels were higher within territories than outside. These 'nectar sources' contrast with the montane territories which were maintained as 'nectar sinks' (standing crops inside lower than outside). The different exploitation strategies of the two populations can be explained by the differences in the timing of nectar production (McFarland 1985).

New Holland Honeyeaters are monogamous, and breeding pairs in Paton's study defended both the nest and adjacent food resources. Territories usually provided enough energy to cover the total energy costs of the nesting pair throughout the breeding cycle. On some occasions, juveniles remained on territories and actively assisted in the defence of flowers. In New England, breeding territories overlapped with the feeding territories. Nesting occurred in autumn and spring, when the climatic impact on nectar predictability was low. With food both abundant and reliable, the breeding birds behaved like those in the richer heathland sites (Table 5). The nest site was the centre of aggression, with only limited use of the surrounding flowers. In both the New England and Victorian populations, feeding territories may be a means by which individuals obtain short-term access to food to ensure overwinter survival and at the same time retain long-term access to breeding sites.

New Holland Honeyeaters may also form dominance hierarchies. A Western Australian site with highly concentrated nectar resources and a high density of New Holland Honeyeaters showed a site-independent dominance hierarchy in the non-breeding

season (Rooke 1979, Table 5). In the breeding season, the site-dependent hierarchy was determined by the proximity of the nest to the resource. In both hierarchical (Rooke 1979) and territorial (Paton 1979) systems, males were dominant over females and adults over immatures.

So, in both nectarivorous and insectivorous guilds of honeyeaters there are frequently sympatric species attempting to forage on the same foods. To gain priority of access to the foods, different species display variations in social behaviour, particularly spacing (Table 6). The different systems in Table 6 represent corners of a many-sided figure with the potential for any intermediate position. Shifts between systems may occur as the importance of different resources changes. Changes in food productivity and distribution, and the presence of other honeyeaters, affect both foraging activity and social behaviour. Faced with differences in the spatial and temporal availability of food, nectarivorous honeyeaters exhibit intraspecific flexibility in social behaviour, while insectivorous species have more stable systems that are interspecifically diverse. However, this may be an artefact of there being a disproportionate number of studies on New Holland Honeyeaters.

IMPLICATIONS FOR CONSERVATION

The information on honeyeater foraging and social behaviour has wider implications in terms of species and habitat conservation. To maintain the diversity of honeyeater species and their social systems, there is a need to protect areas that possess a spectrum of food resources from rich to poor. Maintenance of floral diversity and the full range of nectarivorous honeyeaters are linked, as they are dependent on each other for food and pollination (Paton 1986). Mosaics of rich and poor areas are also needed for insectivorous honeyeaters. Solitary, well-spaced and specialist foragers can occupy less productive patches, while the more aggressive, group-forming species monopolise sites of higher quality (Wykes 1985).

Habitat modification, particularly deforestation, can have an impact on honeyeater communities. Occasionally, vegetation alterations can lead to increased bird densities and species numbers, e.g. honeyeater abundance was greater in a re-vegetated mine-site than in healthy forest (Collins et al. 1985). Alternatively, selective clearing of eucalypt woodlands and montane rainforests may have caused the decline in numbers of Regent and Eungella Honeyeaters, respectively (Franklin et al. 1989, Longmore pers. comm.). The creation of open woodlands by clearing for grazing favours the expansion of Noisy and Yellow-throated Miner colonies (Ford & Bell 1981, Joseph 1986). The impact of the aggressive Noisy Miner is seen in the negative correlation between miner density and the abundance and diversity of other woodland birds in forest patches in Victoria (Loyn 1987) and New South Wales (Ford pers. obs.). Yellow-throated Miners, through competition and interbreeding, appear to have swamped Black-eared Miner colonies within the latter's now disturbed and fragmented mallee habitat (Joseph 1986). Similarly, Wykes (1985) noted that the combination of habitat degradation and invasion by the highly competitive Bell Miner seriously threatens the remnant populations of the rare Helmeted Honeyeater (a well-differentiated subspecies of the Yellow-tufted Honeyeater).

Once established, miners may modify their habitat. By excluding competitors and using harvesting techniques, Bell Miners maintain high densities of psyllids within their

TABLE 6 – Summary of the strategies used by honeyeaters, as either individuals or groups, to gain priority of access to food resources; ^a other means of exploitation include morphological specialisation and use of traplining behaviour; the level of exclusiveness achieved depends on how effectively the honeyeater uses these characteristics.

Degree of exclusiveness	Temporal scale	Spatial scale	Terminology	Honeyeater example (Reference)
High	Short-term	Large area	(Moving territory)	Single: Fuscous (Dunkerley 1989) Group: Yellow-plumed (Immelmann 1961)
High	Short-term	Small area	(Individual space)	Single: Eastern Spinebill (McFarland 1983)
High	Long-term	Large area	(Territory)	Single: New Holland (Paton 1979, McFarland 1986b) Group: Bell Miner (Swainson 1970, Loyn et al. 1983)
Low	Long-term	Small area	(Site-independent hierarchy)	Single: non-breeding New Holland (Rooke 1979)
Low	Long-term	Small area	(Site-dependent hierarchy)	Single: breeding New Holland (Rooke 1979). Group: male groups in Noisy Miner colony (Dow 1978, 1979a,b)
Low	Short-term	Large area	(Swamping)	Aggregations of single birds: Eastern Spinebill (McFarland 1985) Flocks: Brown-headed, Yellow-faced (Paton 1979, Wykes 1985)
Low-high	Long-term	Large area	(Exploitative - high foraging efficiency) ^a	Single: Eastern Spinebill (McFarland 1985, 1986a).

colonies (Loyn et al. 1983). This can lead to tree mortality, increased litter loads and a greater susceptibility to fire. Once the trees begin dying, psyllid numbers fall, the miners move away and the habitat is left to recover as best it can. The declining quality of woodlands dominated by Noisy Miners is also well known (Ford & Bell 1981, Loyn 1987). Whether this situation is a natural 'boom and bust' cycle is unknown. However, because of widespread reduction and fragmentation of forests (see papers in Saunders et al. 1987), the continuation of such activities by these honeyeaters can have detrimental consequences on the remnants of native vegetation and their associated faunas. A pattern of denser woodland patches with shrubs in farmland might better conserve the avian diversity, including honeyeaters, than more evenly thinned and grazed woodland.

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SEXUAL DIFFERENCES IN RESOURCE ACQUISITION BY MIGRANT HUMMINGBIRDS

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ABSTRACT. Data on migrant Rufous Hummingbirds *Selasphorus rufus* suggest that females, especially immatures, may be disadvantaged in obtaining and maintaining feeding territories in the presence of their immature male rivals. Males tended to secure a disproportionate number of territories more quickly and occupied areas of higher flower density. They also were more successful at expanding their territories aggressively upon flower reduction, and were displaced less often than females. Perhaps, in consequence, immature females lagged behind males and migrated through our study site toward the end of the flowering season. However, our data on whether females spent more time on refuelling stopovers or resumed migration later or at lower weight than males were inconsistent. The possibility that immature females compensate for their territorial disadvantage by greater foraging efficiency remains open.

Keywords: Hummingbirds, territoriality, feeding territories, sexual differences, female disadvantage, male advantage, resource acquisition, migratory stopover, flower reduction.

INTRODUCTION

Sexual differences in resource use have been reported for a variety of animal species (Selander 1966, Temeles 1986), yet the reasons for these differences remain poorly understood and controversial (Lewin 1985). Two hypotheses attempt to explain sexual differences in resource use during the non-breeding season. The "Exploitation Hypothesis" states that sexes use different resources because they differ in body size and/or morphology; each sex prefers resources most suited to it (Selander 1966, Peters & Grubb 1983, Temeles 1985). In contrast, the "Interference Hypothesis" maintains that sexes differ in resource use because of social dominance (sometimes conferred by differences in size or morphology). In this case, one sex aggressively displaces the other from mutually-preferred resources through interference competition (Gauthreaux 1978, Temeles 1986). As a result, the subordinate sex subsists on resources outside its preference.

To date, several studies provide indirect support for the Interference Hypothesis (Wolf 1975, Kodric-Brown & Brown 1978, Peters & Grubb 1983, Kuban et al. 1983, Hepp & Hair 1984, Temeles 1986). Two studies (Kodric-Brown & Brown 1978, Temeles 1986) suggest that the superior interference ability of the dominant sex in the acquisition of preferred resources may be offset by a superior exploitative ability of the subordinate sex in the utilization of less preferred resources. Thus, the Exploitation and Interference Hypotheses are not necessarily mutually exclusive.

Data are lacking on the relative abilities of males and females to acquire and exploit resources. Such data are necessary to test basic assumptions of the Exploitation and Interference Hypotheses, i.e. that sexes differ in foraging and/or territorial abilities. Here we offer some relevant data on migrant Rufous Hummingbirds *Selasphorus rufus*, which we studied in California for 11 summers (1976 - 1986).

Rufous Hummingbirds migrate during the summer from their breeding grounds in the Pacific Northwest to their wintering areas in Mexico (Phillips 1975). En route, both sexes stop periodically in mountain meadows, establish vigorously-defended territories around patches of flowers, and require one to two weeks to replenish their 1-2 gram migratory fat store from flower nectar before resuming their journey (Carpenter et al. 1983). Adult males migrate one to four weeks before females and immatures (Phillips 1975, Calder 1987), so females contend mainly with immature males during most of the summer migration. Because we captured significant numbers of adult males at our site in only one year, we are eliminating them from this analysis.

We have argued (Carpenter et al. 1983, Hixon et al. 1983, Paton & Carpenter 1984, Hixon & Carpenter 1988) that this species is selected to minimize the time spent on migratory stopovers, and thus to maximize the rate at which refattening occurs on feeding territories. Our birds act in ways consistent with energy maximization, in terms of territory size adjustments, time budgeting, foraging patterns, meal size, and mass gain (Carpenter et al. 1983, Hixon et al. 1983, Karasov et al. 1986, Hixon & Carpenter 1988, Carpenter & Hixon 1988). The selection pressures for maximization of daily net energy gain in Rufous Hummingbirds should operate equally on males and females, and consistent with this, both sexes defend feeding territories during migratory stopovers.

Body masses of the sexes are similar (male = 3.2 g, female = 3.4 g, Johnsgard 1983), but males have shorter wings and hence a 15% higher wing loading (0.044 g.mm^{-2}) than females (0.038 g.mm^{-2}). Wing lengths do not overlap (Johnsgard 1983, Temeles unpubl.). Feinsinger & Chaplin (1975) argued that higher wing loading increases the cost of flight but also improves agility and therefore enhances territorial ability, enabling monopolization of the densest flower patches. Dense flower patches should be preferred because travel costs among flowers would be reduced.

Indeed, Kodric-Brown & Brown (1978) noted that Rufous Hummingbird males defended territories of higher flower density than females. They suggested that the lower wing loading of females relegated them to sparser patches of flowers, but that their lower cost of flight compensated for the concomitantly longer foraging flight distances. If the Interference Hypothesis holds, males with their higher wing-loading should acquire territories more rapidly, occupy areas with the densest patches of flowers, acquire mass more rapidly and either depart sooner or leave fatter than females. Females, if given the opportunity, should also hold feeding territories in dense patches of flowers. Since our study site is midway along the migration route to Mexico, and most birds will have made at least one refattening stopover by the time they reach us, we would expect females to lag behind males if females refatten more slowly.

On the other hand, if the Exploitation Hypothesis holds, females, with their lower wing-loading, should gain mass at comparable rates to males, even when defending poorer territories. In this case, males and females should show little difference in rates and

amounts of mass gain and length of time required to fatten for the next migratory flight.

METHODS

Our study site was a 2 ha meadow at the base of the east slope of the Sierra Nevada, 27 km NW of Bishop, California. This meadow contains the hummingbird-visited Indian paintbrush, *Castilleja linariaefolia* (Scrophulariaceae), which flowers from mid-July to late August or early September.

In most years, Rufous Hummingbirds arrived between late July and early August. At any one time, up to 50 exclusive territories were established in the 2 ha of flowers. We mist-netted the birds, weighed them, identified their sex and age class (Stiles 1972, Johnsgard 1983), and colour-marked them with narrow strips of coloured surveyors' flagging tape glued to the skin of the back. These strips did not add detectably to their mass or bother them.

In 1979, 1985 and 1986, we halved the number of flowers experimentally on several territories and measured the response of the owners. Each manipulated bird was paired with a control bird. For one to two days before and after flower reduction, we collected data on territory area, number of included flowers, and body masses in some cases (methods in Hixon et al. 1983, Carpenter et al. 1983). These birds were then studied until they resumed migration, which was often behaviourally conspicuous. In addition to experimental flower reduction, unusually hot temperatures during 1980, 1985 and 1986 caused flowers to decline naturally, in some areas quite rapidly.

We counted flowers along two permanent 2-m wide transects (one 36 m long; one 50 m long), one to four times each summer. In seven years from 1980 to 1986, we mapped all territories in the meadow and identified the age and sex class of the owners.

RESULTS

We caught and tagged 200-400 individuals over each summer; 5-35% of these established territories, and up to 80% of the territory owners were marked at any one time. About 85% of our netted Rufous Hummingbirds were immatures and 15% adult females.

Under which resource conditions did different sex and age classes establish territories?

The El Nino years of 1982-1983 were anomalous in that this normally aggressive species defended few territories (Carpenter 1987, 1989). In all other years, most flowers were intensely defended (Carpenter 1978, 1987, Carpenter et al. 1983, Hixon & Carpenter 1983, 1988, Paton & Carpenter 1984). In these years, the numbers of non-territorial birds caught in the meadow always exceeded the numbers of territorial birds, suggesting that the numbers of flowers generally were limiting. Nonetheless, members of all sex and age classes held territories.

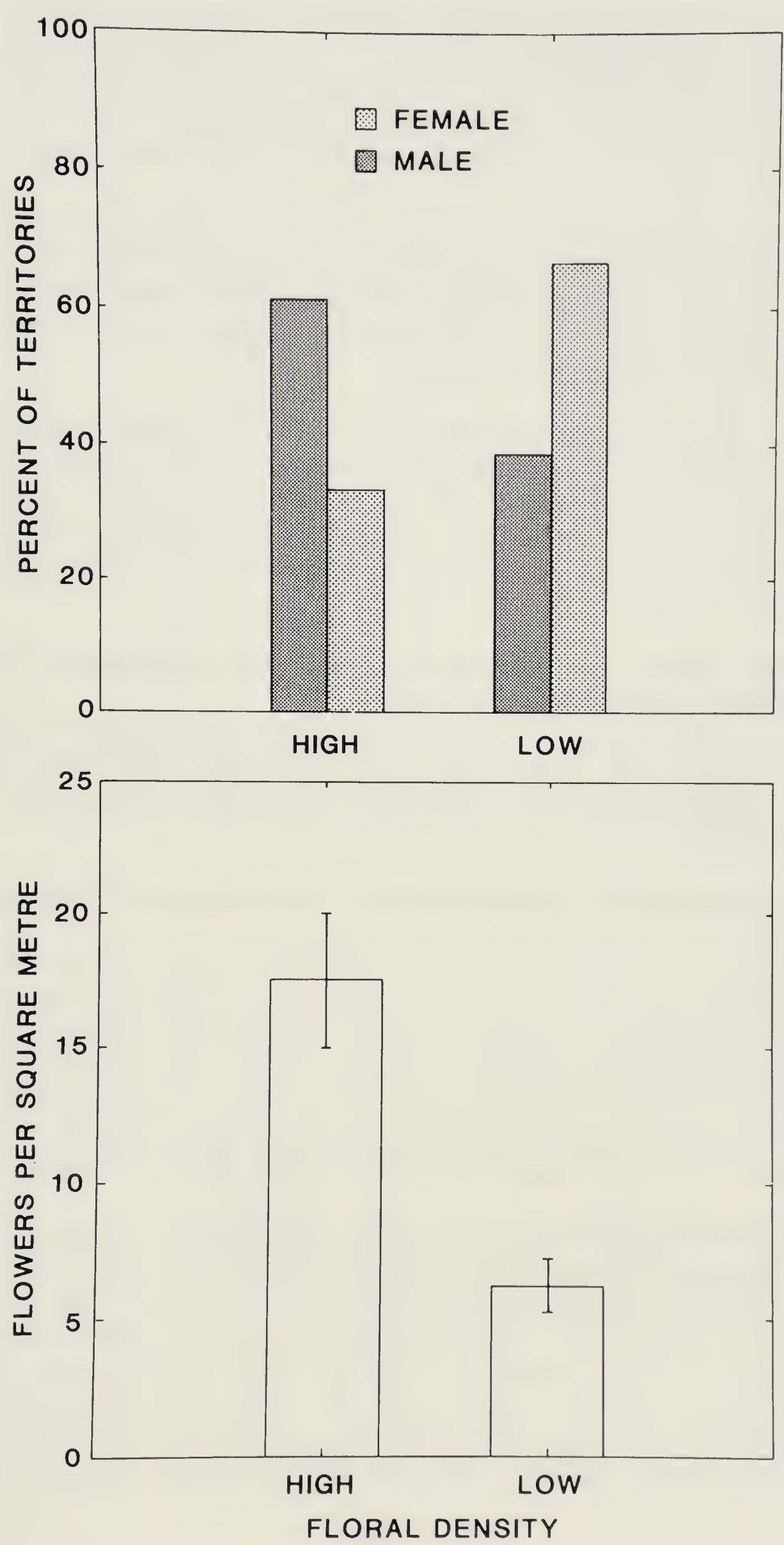


FIGURE 1 – Flower densities occupied by males and females 1980-1986. Top: percent of territories defended by males and females in the vicinity of the high and low flower-density transects; bottom: flower densities (mean flowers.m⁻² ± 1 S.E., data not transformed) were measured along permanent transects in two sites, one (“high”) with higher flower density than the other (“low”).

The probability of establishing a territory depended on age and sex class. Combined data from 1980-1986 indicated that 58 of 250 marked adult females (23%), 123 of 816 immature males (15%), and 82 of 751 immature females (11%) established territories ($G = 21.9$, $N = 1817$, $df = 2$, $P < 0.001$). Thus, relative to their proportions in the netted population, more males and adult females secured territories than immature females.

One measure of ability to obtain a territory is when one bird displaces another from its territory. Of seven takeovers observed involving birds of known age and sex, five displaced birds were immature females. Immature males were never displaced by females, and did five of the seven displacements. Hence, immature males may be better at obtaining territories than females.

We compared territory quality between sexes by assessing their distributions in two parts of the meadow that consistently differed in flower density in 1980-1986 (paired t-test on log-transformed data, $t = 7.06$, $df = 6$, $P < 0.001$; Figure 1, bottom). Combined data from all years indicated that immature males tended to defend territories in areas of higher rather than lower flower density, whereas the reverse was true for females (Figure 1, top; $G = 11.4$, $N = 146$, $df = 1$, $P = 0.001$).

What were the relative abilities of different sex and age classes in maintaining territories when flower density declined?

Following reductions in flowers, immature males often were capable of aggressively expanding their territories and females were not (Table 1). Whenever females did expand their territories, expansion was passive into undefended areas that had been abandoned recently.

Were there costs of lower territorial ability to females or did they compensate exploitatively?

Our netting data indicated that the relative proportions of sex and age classes changed over the summer in our area. In five of the six years for which we had adequate data, the proportion of netted immature males and adult females peaked early in the season and declined thereafter. In contrast, that of immature females increased, peaking late in the season (Figure 2). These observations suggest that immature females may have been delayed in migration, possibly due to subordinate status and inferior abilities in territory acquisition relative to other sex/age classes.

If immature females were delayed, we would expect them to require more time to secure territories and to gain body mass and/or to resume migration at lower body masses than immature males. We recorded the best, most continuous meadow maps in two years, 1980 and 1981. These two years combined showed that most males required one day or less to establish a territory, whereas significantly more females required two days or more ($G = 6.30$, $N = 73$, $df = 1$, $P = 0.01$). When we included the less accurate data from 1982-1986, which had time gaps in the records, the same trend occurred, but the difference was not significant ($G = 2.57$, $N = 155$, $df = 1$, $P = 0.11$).

Longer pre-territorial periods in females may have delayed gains in body mass. Once birds obtained territories, they gained about 0.2 g.day^{-1} (Carpenter et al. 1983), but birds without territories did not gain mass (mean = $0.0 \text{ g.day}^{-1} \pm 0.2 \text{ g.day}^{-1}$ SD, $N = 19$). These two factors alone could explain the migratory lag in immature females.

TABLE 1 – Responses of different sex/age classes to changes in flower abundance. “Aggressive” expansion involves expropriation of defended flowers; “passive” expansion involves annexation of undefended flowers. Data include experiments and natural flower declines in 1979, 1985, and 1986, and natural flower decline in 1980.

Treatment	Response of birds		
	Aggressively expanded territory boundaries	Passively expanded territory boundaries	Did not successfully expand boundaries
Flowers decreased experimentally	2 immature males	2 immature males	0
		1 adult female	
		3 immature females	
Flowers decreased naturally	3 immature males	10 immature males	2 immature males
		4 immature females	4 immature females
			2 adult females

We monitored the masses of all 1985 and 1986 experimental birds until they resumed migration. Among individuals whose flowers were experimentally halved, the one immature male continued to gain mass at high rates, whereas the one adult female and two of three immature females experienced severe reductions in mass gain or even mass loss.

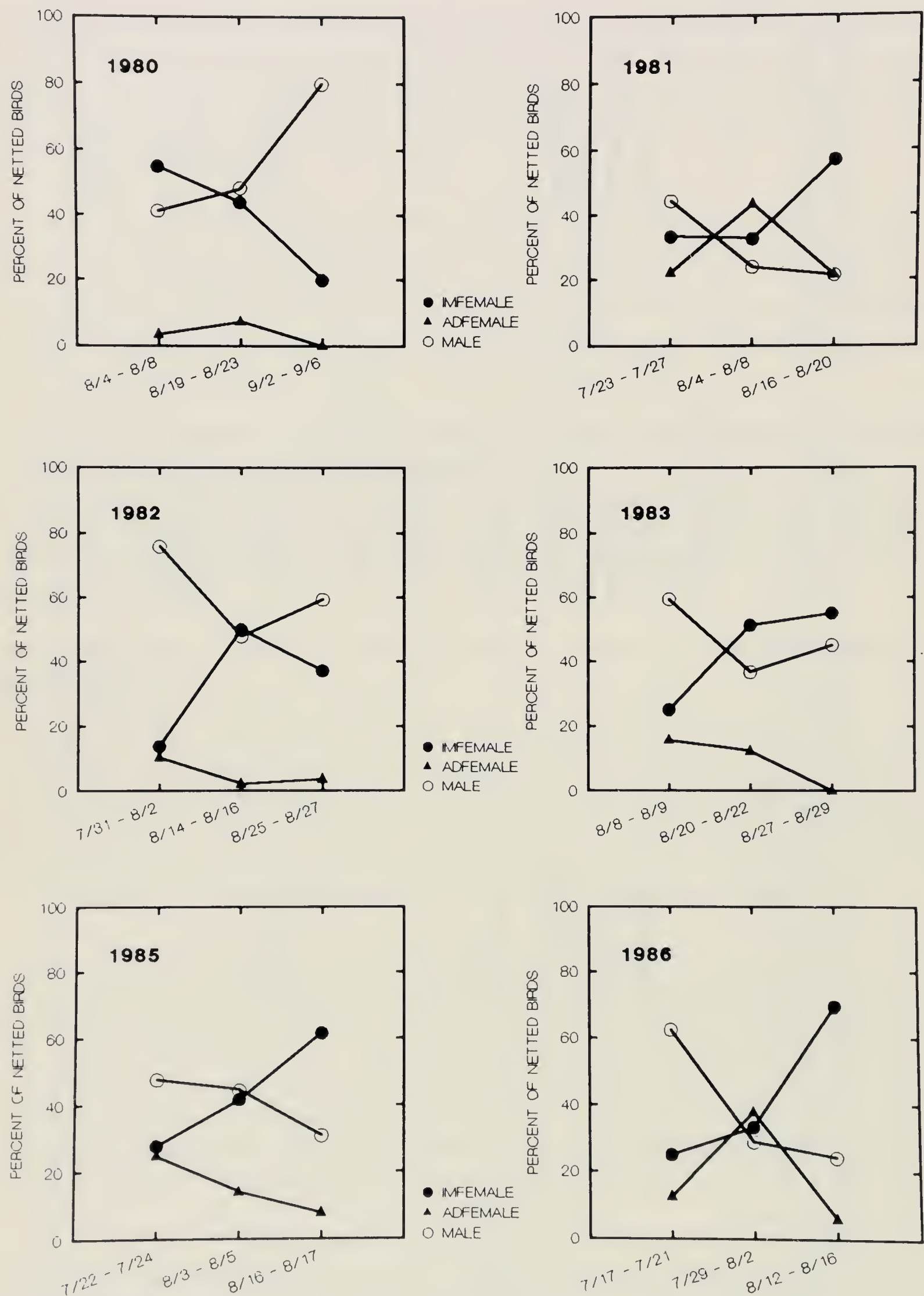


FIGURE 2 – Changes in the relative proportions of different sex-age classes over the season. Data from 1984 are not included because we missed both the beginning and end of the season that year.

However, when we combined all data, age/sex classes did not differ either in total stopover time (one-way ANOVA, $F_{2,223} = 1.25$, $P = 0.29$) or in final body mass the evening before migration (one-way ANOVA, $F_{2,53} = 1.13$, $P = 0.33$). Therefore, our data do not unequivocally show that females suffered a cost in terms of delayed refattening.

In 1980 and 1981, we recorded the identities of persistent intruders that robbed from other birds' territories. Of 19 such birds, 15 were female (10 immatures, 4 adults, 1 undetermined).

DISCUSSION

Our data suggest that Rufous Hummingbird females, primarily immatures, have lower territorial ability relative to immature males. Immature females obtain and defend territories, but relative to males they: 1) require longer to obtain a territory, 2) secure proportionately fewer territories, and 3) are displaced from their territories more often.

This lower territorial ability is associated with defence of territories with sparser flowers on average, and with lower ability to maintain territory size and mass gain in the face of declining flowers. These factors may cause immature females to lag behind immature males along the migratory route. However, our data on whether the territorial disadvantage of immature females translates into an overall migratory disadvantage were contradictory. We cannot discount the possibility that the energetic advantage of lower wing-loading could compensate them exploitatively on stopovers, for example, by permitting successful robbing, and that they merely leave the breeding grounds later than any other age/sex class. This alternative should be explored.

Our data suggest that adult females are intermediate in territorial ability between immature males and immature females. Relatively more adult females secure territories than the other two age/sex classes, yet our few experimental data suggested that they are less able than immature males to expand territories when necessary. Their low wing-loading should confer a disadvantage in "fighting" ability relative to immature males, but their greater experience and colouration could confer advantages over immature females. Immature male and adult female Rufous Hummingbirds both have a patch of iridescent red feathers on the throat and considerable rufous colouration at the base of the tail (Stiles 1972). In contrast, immature female birds are much less brightly coloured. Ewald & Rohwer (1980) demonstrated that drab individuals of another colour-polymorphic species have to chase intruders more frequently and longer to maintain their territories than do brightly-coloured individuals.

Thus, immature males may have a double advantage, bright colour and short wings, whereas immature females are doubly disadvantaged in territorial encounters. Adult females could help distinguish whether colour or wing-loading is more important in aggressive ability, since they are as brightly coloured as immature males, but have wing-loading as low as immature females. If colour is more important, their aggressive abilities should approach those of immature males. If wing-loading is more important, their abilities should approach those of immature females; and if both factors are important, their abilities should fall in between. This hypothesis awaits a rigorous test.

The patterns in our data are thus consistent with the hypothesis that interference is the primary factor causing differences between the sexes in resource use during southward migration. Whether females compensate by higher exploitative efficiency remains an open question.

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RESOURCE PARTITIONING WITHIN AUSTRALIAN NECTARIVOROUS BIRD COMMUNITIES

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ABSTRACT. Nectar-feeding birds such as honeyeaters usually occupy habitats in which the distribution of particular plant species, individual plants and flowers is patchy. The contribution that each species makes to the overall nectar pool is dependent upon plant density, floral abundance and amount of nectar produced per flower. Interspecific partitioning of nectar resources is common, with the largest honeyeater species at a given site generally relying upon the most productive plant species and flowers, whereas smaller, subordinate birds are obliged to make some use of less rewarding sources of energy. By foraging in this manner, all birds manage to achieve overall energy balance.

Keywords: Resource partitioning, nectarivorous birds, honeyeaters, preferential foraging, flowers, nectar, pollen, Australia.

INTRODUCTION

Honeyeaters (Meliphagidae) are the most abundant Australian nectarivorous birds, occupying habitats that range from eucalypt forest to proteaceous heath (Collins & Paton 1989). Several species co-occur in most habitats, each making some use of nectar, although the relative importance of this and other foodstuffs varies according to the species, location and time of year (Pyke 1980, Collins et al. 1990).

The spatial patchiness of nectar resources in honeyeater habitats is well documented, and occurs primarily because of the uneven distribution of individual plants, variable numbers of flowers on these plants, and the differing capacities of constituent species to produce nectar (Collins & Rebelo 1987, Collins & Grey 1989). Nectar availability at these sites also varies with time. For instance, failure of nectar production to match nectar depletion by honeyeaters and other animals often means that standing crops are smaller at dusk than earlier in the day (Ford & Paton 1982, Collins et al. 1990). Nectar availability also decreases as flowers age, and the overall contribution made by a particular plant varies according to its flowering phenology (Collins 1985, Collins & Newland 1986, Collins et al. 1990).

Evidence gathered in many parts of Australia suggests that honeyeaters often forage selectively for nectar, preferring plant species, patches of these species, individual plants and flowers that make foraging most profitable (Paton & Ford 1983, Collins & Newland 1986, Collins & Grey 1989, Collins et al. 1990). This paper describes some of the ways in which honeyeaters in two Western Australian habitats partition nectar resources, and interprets these observations in terms of likely energetic benefits for the birds involved.

METHODS

Investigations reported here were undertaken at two sites within the southwest botanical province of Western Australia. The first of these is an 8.5 ha portion of sclerophyllous forest, approximately 9 km south of Jarrahdale. Vegetation at this site has been described by Wykes (1985) and Collins & Newland (1986), and is dominated by *Eucalyptus marginata* (jarrah) and *E. calophylla* (marri), with understorey and shrub layers comprising *Dryandra sessilis*, *Grevillea wilsonii*, *Adenanthos barbigera* and *Dryandra nivea*. The abundance of these species was estimated using the plotless, point-centred quarter method developed by Mueller-Dombois & Ellenberg (1974) (see Collins 1985 for details).

The second site used in this study is a 10 ha remnant of heathland surrounded by cleared farmland, approximately 10 km north of Watheroo. Other than *Eucalyptus rhodantha*, the most abundant plants are *Banksia prionotes* and *Dryandra ashbyi* (McNee 1986). Plant densities were not estimated quantitatively at this site.

The most frequently observed honeyeaters at the Jarrahdale site were *Anthochaera chrysoptera* (Little Wattlebird), *Phylidonyris novaehollandiae* (New Holland Honeyeater) and *Acanthorhynchus superciliosus* (Western Spinebill). At the Watheroo site, *Lichenostomus virescens* (Singing Honeyeater), *Lichmera indistincta* (Brown Honeyeater) and *Manorina flavigula* (Yellow-throated Miner) were most abundant (Collins & Newland 1986, McNee 1986).

Morphological and other changes associated with the floral development of *D. sessilis* and *G. wilsonii*, and *E. rhodantha*, were recorded at Jarrahdale and Watheroo, respectively, during 1984 and 1986 (see McNee 1986, Collins & Grey 1989 and Collins et al. 1990 for details). This information was then used as a basis for distinguishing between different age-classes, and the number of flowers or inflorescences in each class counted for patches of at least 20 *D. sessilis*, *G. wilsonii* and *E. rhodantha* plants in June, September and June, respectively.

The patches of vegetation mentioned above were observed for three hours from dawn on each of three successive days during June or September. During this time, each visit by a honeyeater to a particular age-class of flower (both sites) or plant species (Jarrahdale only) was recorded (Collins 1985, McNee 1986, Collins et al. 1990). Additional evidence relating to plant species visited by honeyeaters was gathered by taking pollen smears from the throats, bills and foreheads of birds captured in mist nets, and comparing these with type pollen from plants which occurred at the study sites (see Collins et al. 1990 for details).

Nectar volumes and sucrose concentrations (w/w) were measured at dawn and dusk for *D. sessilis* and *G. wilsonii* flowers until these began to senesce. The energy content of each sample was estimated in the manner described by Collins & Newland (1986). Energy expenditures incurred by honeyeaters while extracting nectar samples were estimated using time budget data presented by Collins et al. (1990) and equations described by Collins & Newland (1986). The foraging efficiencies of these honeyeaters were then calculated as the difference between nectar energy intake and energy expenditure (Collins et al. 1990).

TABLE 1 – Gross changes in *Dryandra sessilis* inflorescences, and *Grevillea wilsonii* and *Eucalyptus rhodantha* flowers, after initial pollen presentation.

Time after initial pollen presentation (days)	Floral colour and morphology		
	<i>Dryandra sessilis</i>	<i>Grevillea wilsonii</i>	<i>Eucalyptus rhodantha</i>
1	Approx. 23% of outer flowers open	Style very hooked, perianth red	Style partly concealed, outer stamens exserted
2	Approx. 71% of outer flowers open	Style straight, perianth red	Style partly concealed, outer stamens exserted
3	Approx. 99% of outer flowers open	Style straight, top edge of perianth black	Style partly concealed, outer stamens exserted
4	All flowers open, outer perianths dark yellow	Style straight, distal half of perianth black	Style partly concealed, outer stamens exserted
5	Most perianths dark yellow, some brown	Style straight, entire perianth black	Style partly concealed, outer stamens exserted
6	Most perianths brown	–	Style exposed, most anthers dehisced and dry
7	All perianths dark brown	–	Style exposed, most anthers dehisced and dry
8	–	–	Style exposed, most anthers dehisced and dry
9	–	–	Style exposed, most anthers dehisced and dry
10	–	–	Stamens progressively lost except for those attached to outer edge of receptacle
20	–	–	Remaining stamens lost
30	–	–	Remaining stamens lost

RESULTS

Floral and plant abundance

Dryandra sessilis inflorescences comprise 90-100 tightly packed cream flowers, each of which has a stigma-nectary distance of approximately 30 mm. The outermost flowers open first, and approximately seven days elapse from the time that the first flower

opens until all flowers have senesced. Morphological and colour changes during floral development are sufficiently discrete to permit easy identification of different-aged inflorescences (Table 1). In June of 1984, the relative percentages of day 1-2, day 3-4, day 5-6 and day 7 inflorescences at the Jarrahdale study site were 34.2, 34.9, 20.8 and 10.1, respectively (Table 2).

Grevillea wilsonii inflorescences are loose racemes of red gullet-shaped flowers, each of which has a stigma-nectary distance of approximately 35 mm. Age-classes of these flowers can be readily distinguished (Table 1), and in September 1984, 73% of the nectar-producing flowers at the study site were 1-2 days old (Table 2).

Development of *Eucalyptus rhodantha* flowers takes up to 30 days, although four distinct age-classes can be differentiated (Table 1). At Watheroo in June 1986, the percentages of day 1-5, day 6-10, day 11-20 and day 21-30 flowers were 32.7, 16.2, 24.3 and 26.8, respectively (Table 2).

The principal nectar-producing plant species in flower at Watheroo in June and July of 1986 were *E. rhodantha*, *Banksia prionotes*, *Dryandra ashbyi* and *Eucalyptus loxophleba* (McNee 1986). At Jarrahdale, the most common species at similar times in 1984 were *D. sessilis* (16.6%), *Adenanthos barbigera* (27.7%), *Grevillea wilsonii* (18.1%) and *Dryandra nivea* (31.8%) (Figure 1).

TABLE 2 – Percentage frequencies of visits by honeyeaters to *Dryandra sessilis*, *Grevillea wilsonii* or *Eucalyptus rhodantha* inflorescences or flowers belonging to different age-classes. N denotes numbers of plants observed. Absolute numbers of flowers/inflorescences in each age-class on these plants, and the numbers of visits by honeyeaters, are given in parentheses. LWB, WS, BH, SH, YTM and NHH denote *Anthochaera chrysoptera*, *Acanthorhynchus superciliosus*, *Lichmera indistincta*, *Lichenostomus virescens*, *Manorina flavigula* and *Phylidonyris novaehollandiae*, respectively.

Plant species and time of year	Age of flowers (days)	Relative abundance of flowers (%)	Percentage frequency of visits by		
			LWB	WS	NHH
<i>Dryandra sessilis</i> (June, N = 150)	1-2	34.2(379)	68.1(64)	55.0(22)	71.0(149)
	3-4	34.9(386)	31.9(27)	35.0(14)	25.7(54)
	5-6	20.8(230)	0.0(0)	5.0(2)	2.4(5)
	7	10.1(112)	0.0(0)	5.0(2)	0.9(2)
<i>Eucalyptus rhodantha</i> (June, N = 124)	1-5	32.7(161)	73.3(44)	11.2(6)	
	6-10	16.2(80)	6.7(4)	18.5(10)	
	11-20	24.3(120)	13.3(8)	40.7(22)	
	21-30	26.8(132)	6.7(4)	29.6(16)	
			LWB	WS	NHH
<i>Grevillea wilsonii</i> (September, N = 20)	1-2	73.1(471)	0.0(0)	100.0(39)	0.0(0)
	3	26.9(173)	0.0(0)	0.0(0)	0.0(0)

Floral and plant selection

Evidence presented in Tables 2 and 3, and Figure 1, suggests that nectar resources are partitioned by honeyeaters at Watheroo and Jarrahdale. For instance, Brown Honeyeaters (c.10 g) were the only birds seen foraging from *E. loxophleba* in July, although these birds, Singing Honeyeaters (c.25 g) and Yellow-throated Miners (c.40 g) all visited *E. rhodantha*, *D. ashbyi* and *B. prionotes*. The relative importance of the latter plants to honeyeaters is unknown, although McNee (1986) has shown that Brown and Singing Honeyeaters visit day 1-5 and day 11-20 *E. rhodantha* flowers more frequently than other age-classes of the same species. Little Wattlebirds (c.60 g) and New Holland Honeyeaters (c.20 g) make almost exclusive use of day 1-2 and day 3-4 *D. sessilis* inflorescences at Jarrahdale, whereas Western Spinebills (c.10 g) also visit older *D. sessilis* inflorescences and young *G. wilsonii* flowers.

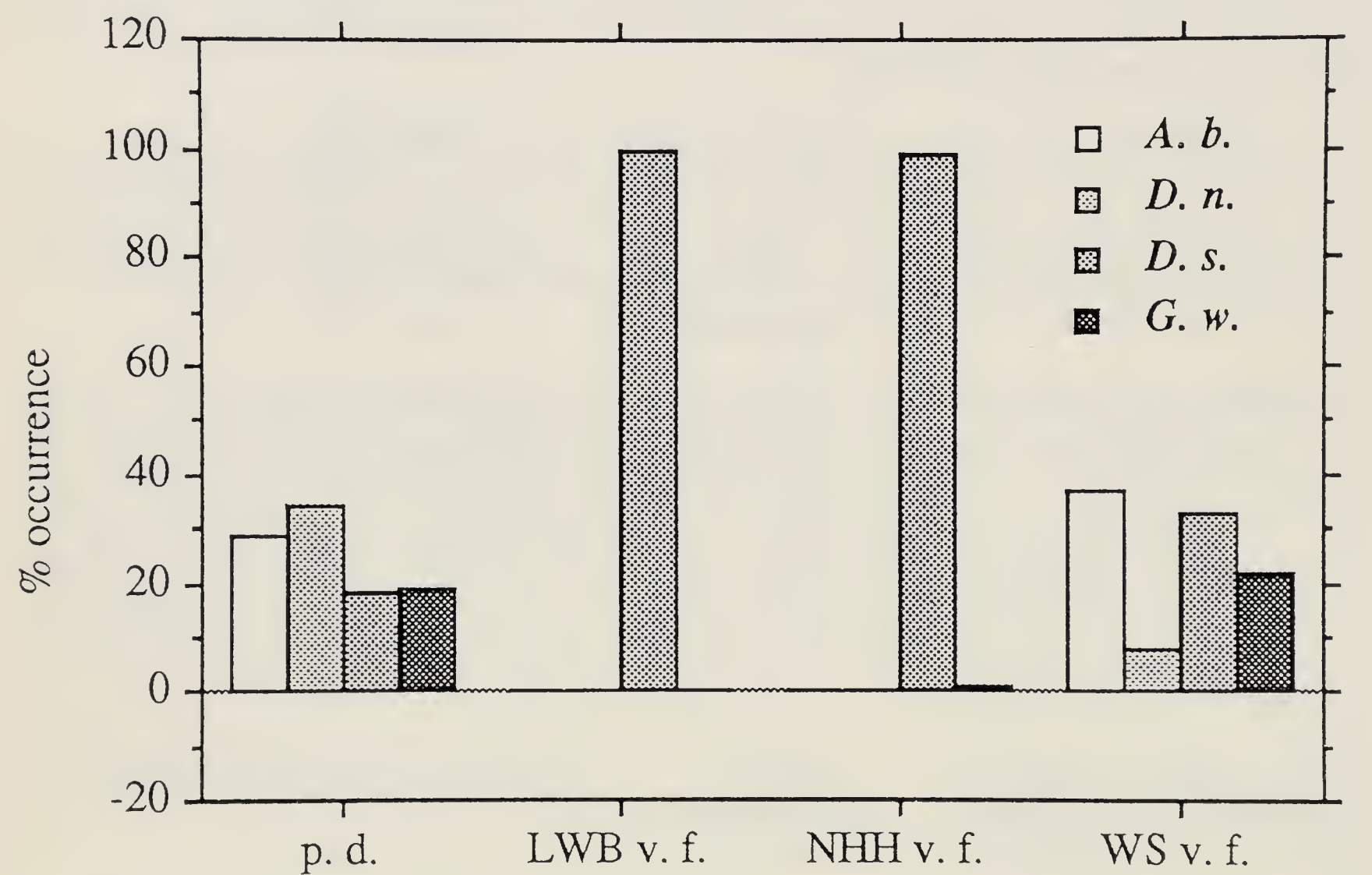


FIGURE 1 – Relative frequencies of visits by honeyeaters to flowers or inflorescences on *Adenanthos barbiger* (*A.b.*), *Dryandra nivea* (*D.n.*), *Dryandra sessilis* (*D.s.*) and *Grevillea wilsonii* (*G.w.*). p.d. denotes the relative abundances of these plant species. LWB, NHH and WS have the same meanings as in Table 2.

Energetic basis for resource partitioning

Nectar energy availability in *D. sessilis* inflorescences and *G. wilsonii* flowers is typically greatest at dawn and lowest at dusk. Values at these times also decrease as flowers age, and nectar production ceases by the time flowers start to senesce (Table 4). Equivalent data for *E. rhodantha* are not presented in this paper, although McNee (1986) has shown that nectar availability is usually greatest at dawn in day 6-10 and day 11-20 flowers.

The efficiency with which honeyeaters forage at *D. sessilis* or *G. wilsonii* is influenced significantly by nectar availability, the species of bird involved and the time (and energy) spent by the bird in obtaining nectar (Table 5). Day 1-2 *D. sessilis* inflorescences at dawn are the most rewarding sources of energy at Jarrahdale in winter and

TABLE 3 – Relative mean occurrence of pollen grains in smears taken from the foreheads and throats of honeyeaters (partly after Collins et al. 1990). Ranges of values are given in parentheses. Unless indicated otherwise, the sexes of birds tested were not known. Abbreviations used to denote honeyeater species are the same as in Table 2.

Plant species and location	Percentage frequency of pollen on		
Watheroo (May)	BH	SH	YTM
<i>Banksia prionotes</i>	74.0(43.9-99.0)	68.1(14.6-99.3)	21.7(17.5-28.2)
<i>Dryandra ashbyi</i>	0.0	0.7(0.0-4.2)	0.0
<i>Eucalyptus rhodantha</i>	25.7(0.0-57.3)	31.0(0.5-85.0)	78.2(71.8-82.5)
Watheroo (July)	BH	SH	YTM
<i>Banksia prionotes</i>	0.7(0.4-1.5)	9.4(0.0-65.4)	13.8(9.9-20.7)
<i>Dryandra ashbyi</i>	18.5(1.9-27.6)	43.8(7.4-99.0)	51.1(0.0-88.9)
<i>Eucalyptus loxophleba</i>	31.1(0.0-64.7)	0.0	0.0
<i>Eucalyptus rhodantha</i>	49.3(7.2-96.0)	46.5(0.6-72.5)	35.1(1.2-89.3)
Jarrahdale (July)	LBW	WS(Male)	NHH
<i>Adenanthos barbigera</i>	0.0	1.2(0.0-3.1)	0.0
<i>Dryandra nivea</i>	0.0	12.1(0.0-15.8)	0.0
<i>Dryandra sessilis</i>	100.0	83.6(79.1-92.7)	95.8(91.4-100)
<i>Grevillea wilsonii</i>	0.0	3.1(0.0-8.1)	4.2(0.0-7.3)

TABLE 4 – Availability of nectar at dawn and dusk on successive days during the development of unbagged *Dryandra sessilis* and *Grevillea wilsonii* flowers (partly after Collins et al. 1990). N denotes numbers of flowers tested.

Plant species and time of year	Time of day		Nectar availability (kJ/flower) on day						
			1	2	3	4	5	6	7
<i>Dryandra sessilis</i> (July, N = 10)	Dawn	X	0.603	0.540	0.284	0.060	0.034	0.007	0.005
		SD	0.031	0.028	0.029	0.018	0.009	0.006	0.003
	Dusk	X	0.065	0.040	0.018	0.012	0.007	0.004	0.004
		SD	0.010	0.013	0.008	0.007	0.004	0.004	0.003
<i>Grevillea wilsonii</i> (July, N = 10)	Dawn	X	0.030	0.026	0.011				
		SD	0.011	0.013	0.007				
	Dusk	X	0.016	0.013	0.004				
		SD	0.007	0.006	0.004				

TABLE 5 – Foraging efficiencies of honeyeaters visiting *Dryandra sessilis* and *Grevillea wilsonii* flowers (partly after Collins et al. 1990). Abbreviations used to denote honeyeater species are the same as in Table 2. Foraging efficiency is the difference between energy intake, assuming 100% ingestion of available nectar when a flower is visited by a bird, and the energy expended in flying to the flower and extracting this nectar; efficiencies have been calculated for situations in which birds had to fly different distances in order to harvest nectar: flight times used were (A) 0.5, (B) 2.0 and (C) 3.5 sec.

Plant species	Age of flower/ time of day	Standing crop energy (J/flower)	Nectarivore species	Foraging efficiency (J)		
				A	B	C
<i>Dryandra sessilis</i>	Day 1/dawn	603	WS	597	593	590
			NHH	594	587	581
			LWB	589	568	548
	Day 4/dawn	60	WS	54	50	47
			NHH	51	44	38
			LWB	46	25	5
<i>Grevillea wilsonii</i>	Day 1/dawn	30	WS	27	24	24
			NHH	26(?)	19(?)	16
			LWB	21(?)	1(?)	-20
	Day 3/dawn	11	WS	8	5	1(?)
			NHH	7(?)	0(?)	- 7(?)
			LWB	2(?)	-18(?)	-39(?)

early spring for all birds, regardless of the time spent in extracting nectar. Unlike small honeyeaters such as Western Spinebills, Little Wattlebirds have difficulty in balancing energy expenditure and gain while foraging at older *D. sessilis* inflorescences or *G. wilsonii* flowers, especially if they are widely-spaced.

DISCUSSION

Plant species present in any given habitat generally differ with respect to the contributions they make to the floral and nectar environments. For instance, the most abundant and uniformly distributed plant species at Jarrahdale is *Adenanthos barbigera*, although each plant usually bears relatively few flowers, most of which produce small amounts of nectar (Collins & Newland 1986). In contrast, *D. sessilis* is less abundant, and often more widely spaced, but has such large numbers of productive inflorescences per plant that its overall contribution to the nectar pool is usually much greater. Nectarivores are thus provided with a range of foraging options. They could respond by harvesting nectar haphazardly, limited only by restrictions imposed by incompatibilities between bill and floral morphologies. Alternatively, they might forage selectively, with their preferred sources of nectar chosen on the basis of plant density, floral abundance per plant, amount of nectar present per flower, or some combination of these parameters (Collins et al. 1990).

According to optimal foraging theory, nectarivorous birds in laboratory or field situations should maximize the net rates at which they acquire energy (Pyke 1984). One way of achieving this objective might be for the birds to select plant species that offer the greatest nectar rewards per plant and/or flower, although there would be some energetic sacrifices if the plants were widely spaced (Table 5). Alternatively, nectarivores might choose species with the greatest plant and floral densities, thereby minimizing the energetic cost of movement between flowers. In some instances, birds might opt for a combination of both strategies, as is the case with Little Wattlebirds and New Holland Honeyeaters at Jarrahdale. Both species forage selectively at *D. sessilis* inflorescences, but also prefer the densest patches of this species and individual plants with the most flowers (Collins 1985, Collins & Grey 1989). Quantitative data relating to plant and species choice are unavailable for the Watheroo site, although general observations reported by McNee (1986) suggest that honeyeaters prefer *Eucalyptus rhodantha* plants that bear the greatest numbers of productive flowers at any given time.

Energy expenditures and requirements of large nectarivores such as Little Wattlebirds or Yellow-throated Miners are greater than those for smaller birds, all other things being similar (Collins & Paton 1989). For this reason, one might expect large nectarivores to be more discerning than others in their choice of nectar resources. Insufficient data are available to test this proposition for honeyeaters at Watheroo, although evidence presented above indicates that Little Wattlebirds and New Holland Honeyeaters use day 1-2 and day 3-4 *D. sessilis* inflorescences almost exclusively at Jarrahdale. Smaller Western Spinebills at the same location also use these sources of nectar, but make frequent visits to older inflorescences and flowers of generally less-rewarding plants such as *Grevillea wilsonii* and *A. barbiger*. By partitioning nectar resources in this manner, large and small honeyeaters are able to achieve overall energy balance.

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ENERGETICS OF COMPETITION AND GUILD STRUCTURE OF NEOTROPICAL HUMMINGBIRDS

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ABSTRACT. Because hummingbirds are very sensitive to energy stress, interspecific differences in short-term energetic success may be an important determinant of local guild composition. I examined the effects of competition on short-term energetic success in a territorialist, *Amazilia saucerrottei* (Steely-vented Hummingbird), and a low-reward trapliner, *Chlorostilbon canivetii* (Fork-tailed Emerald), in cage experiments that simulated varying conditions of competition, nectar availability, and flower dispersion. When birds shared an *ad libitum* food source, each participant suffered significant negative energetic effects relative to birds tested alone. This energy competition was asymmetrical, with behaviourally dominant individuals or species experiencing less energy stress than their cagemates. When heterospecific pairs competed for limited food, the territorialist experienced less energy stress than the trapliner for both clumped and dispersed arrangements of five feeders. The trapliner was somewhat less energy-stressed when feeders were dispersed rather than clumped, but failed to maintain energy balance at either treatment.

Keywords: Tropical hummingbirds, guild dynamics, foraging energetics, competition, foraging strategy.

INTRODUCTION

Neotropical guilds of nectar-feeding birds often contain many hummingbird species, and the composition of a local guild may change over seasons or even days (Feinsinger 1976, Stiles 1980, Feinsinger et al. 1985). One mechanism contributing to this dynamic structure may be species-specific changes in short-term energetic success in response to shifts in climate or food resources. Species within a guild may use distinct foraging modes, each of which may respond differently in their energetic costs and benefits to variation in food availability and competitor pressure (Feinsinger et al. 1979). Hence, local guild composition at a given time should in part be determined by the relative energetic success of the potential member species.

To test the hypothesis that foraging modes differ in energetic success as a function of ecological conditions, I studied the hummingbird guild in Monteverde, Costa Rica. I focused on two short-billed species that are similar in body size and bill morphology, co-occur for much of each year, visit many of the same flower species, and yet exhibit divergent foraging modes. The Steely-vented Hummingbird *Amazilia saucerrottei* * is a mid-sized (3.5-4.9 g) territorialist that defends clumps of flowers. It has high wing disc loading ($.0335 \text{ g.cm}^{-2}$, Feinsinger et al. 1979), which may enhance acceleration and manoeuvrability but results in relatively high flight costs. The Fork-tailed Emerald *Chlorostilbon canivetii* is a somewhat smaller (1.8 - 3.0 g) "low-reward trapliner" that visits many of the same flower species as the Steely-vented Hummingbird, as well as many flowers not often visited by other hummingbirds. The Emerald may visit low-density flowers by following a regular route or "trapline" that is repeated

* Common and scientific names follow Stiles & Skutch (1989).

throughout the day. The Emerald has low wing disc loading ($.0262\text{ g.cm}^{-2}$, Feinsinger et al. 1979), and hence relatively low flight costs which may be energetically advantageous when flowers are far apart. These two species interact frequently in the field, and when territorial birds are defending rich nectar sources, the Emerald appears restricted to flowers that are widely dispersed (Feinsinger 1976).

FLIGHT-CAGE EXPERIMENTS

Experiment 1: competition for defensible unlimited food

METHODS. The experimental design included three factors: species, number of birds (1 or 2), and pair type (conspecific or heterospecific), for a total of eight treatment combinations. I ran a total of six replicates per species for each type of competition. Each trial ran 48 hours and consisted of a control day (solitary birds, each with its own ad libitum feeder of 20.0% sucrose solution), followed by an experimental day (paired birds sharing a single ad libitum feeder).

I recorded behavioral interactions and foraging behavior, and calculated energy budgets (intake [food] = expenditure [respiration] + storage [biomass production]) as mass-specific rates using a gravimetric method (Tiebout 1989). I considered rates of energy storage to be the best single measure of energetic success. A bird that won a majority of agonistic encounters was scored as winning control of the feeder for a given 2 hrs observation period, with the cagemate scored as losing. Behaviour and the energy budget for each bird of a pair were compared with those of the previous control day using a repeated-measures ANOVA, and differences were assumed to be due to interactions between cagemates.

RESULTS. For both pair types, behavioural winners had higher energetic success than their cagemates. However, winners and losers both experienced energetic consequences compared with solitary birds (Table 1). Losers experienced significant increases in meal size, interbout time (interval between feeder visits) and hover time, with a strong trend towards increased energy expenditure. Most importantly, their energy storage rates dropped $101\text{ J.g}^{-1}.\text{h}^{-1}$ below control levels. Winners experienced only one significant response, an increase of $34\text{ J.g}^{-1}.\text{h}^{-1}$ in their intake rates compared with controls.

TABLE 1 – Behavioural and energetic consequences of interference competition for an unlimited food source. Solitary birds (control = C) were compared with birds in pairs (experimental = X) using a matched-pairs t-test. Data for the Steely-vented Hummingbird and the Fork-tailed Emerald are combined (3 observation periods per trial, 72 trial periods per species). See text for definitions of lost and won. Difference (Δ) calculated as: $\Delta = X - C$. * = $P < 0.05$, ** = $P < 0.01$, T = $0.1 > P > 0.05$, NS = $P > 0.1$.

Variable	Lost (N=32)		Tied (N=8)		Won (N=32)	
	Δ	P	Δ	P	Δ	P
Meal size (mg)	+39	*	-10	NS	-3	NS
Interbout (min)	+8	**	0	NS	+1	NS
Hover time (%)	+10	*	+10	NS	+5	NS
Intake ($\text{J.g}^{-1}.\text{h}^{-1}$)	-36	NS	-15	NS	+34	*
Expenditure (")	+65	T	+57	NS	+46	NS
Storage (")	-101	**	-131	NS	-13	NS

Interspecific competition was highly asymmetrical. Steely-vented Hummingbirds suffered very few negative consequences as a result of sharing a feeder with an Emerald, whereas the latter paid a high energetic price. In heterospecific pairs, both species increased hover time about 11% relative to controls, with an associated increase in energy expenditure of about 13%. The territorialist was able to compensate for increased expenditure with an equivalent increase in energy intake, whereas the subordinate trapliner could not. Birds in conspecific pairs (Figure 1A) experienced energetic consequences intermediate to birds in heterospecific pairs (Figure 1B), and conspecific pairs of each species were approximately equivalent in their energetic success.

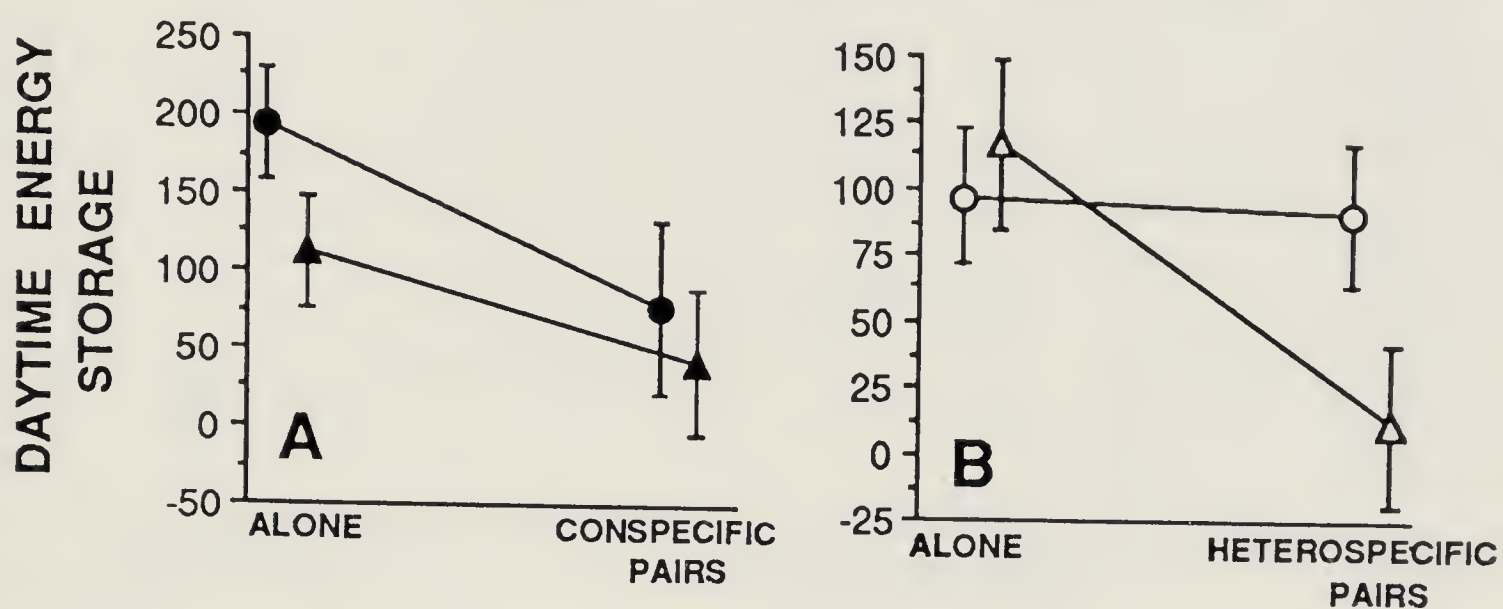


FIGURE 1 – Daytime energy storage rates (J.g⁻¹.h⁻¹) for hummingbirds feeding from an unlimited food source. Data for conspecific pairs (A) and heterospecific pairs (B) of the Steely-vented Hummingbird (*Amazilia*, circles) and the Fork-tailed Emerald (*Chlorostilbon*, triangles) have been shown separately.

Experiment 2: variation in flower dispersion

METHODS. Heterospecific pairs were tested for one foraging day (dawn to dusk) in a flight cage 20 m long. I delivered 20.0% sucrose solution to five feeders at rates approximately 60-70% of normal ad libitum feeding levels. In the clumped treatment, all five feeders were close together and easily defensible from the nearest of five available perches. In the dispersed treatment, the feeders were evenly spaced throughout the cage, such that only one feeder was defensible from a given perch. I recorded behaviour as above, and I measured energy budgets using the doubly labeled water (HTO-18) method (Tiebout & Nagy 1990).

The territorialist obtained slightly more food when it could successfully defend feeders (clumped feeders) than when it could not (6.92 vs. 6.61 kJ.g⁻¹.day⁻¹, respectively). The trapliner had a somewhat higher intake when feeders were indefensible (dispersed) than when not (7.92 vs. 6.79 kJ.g⁻¹.day⁻¹, respectively; $P = .06$ for both comparisons). Regardless of feeder dispersion, the territorialist maintained energy balance by keeping expenditures at or below intake levels (Figure 2). In contrast, the trapliner consistently expended more energy than it took in, with consequent depletion of energy stores.

Both species changed their foraging behavior over the course of the day in ways that tended to reduce competition and enhance profitability. In general, birds decreased both flight time and visit rate over the day. In addition, both species significantly reduced the overlap and the diversity of feeders visited throughout the foraging day,

tending to concentrate on a subset of feeders not visited by their cagemate (see Gill 1988) (Figure 3). Thus, birds tended to reduce the energetic consequences of competition and foraged with increasing profitability as the day progressed.

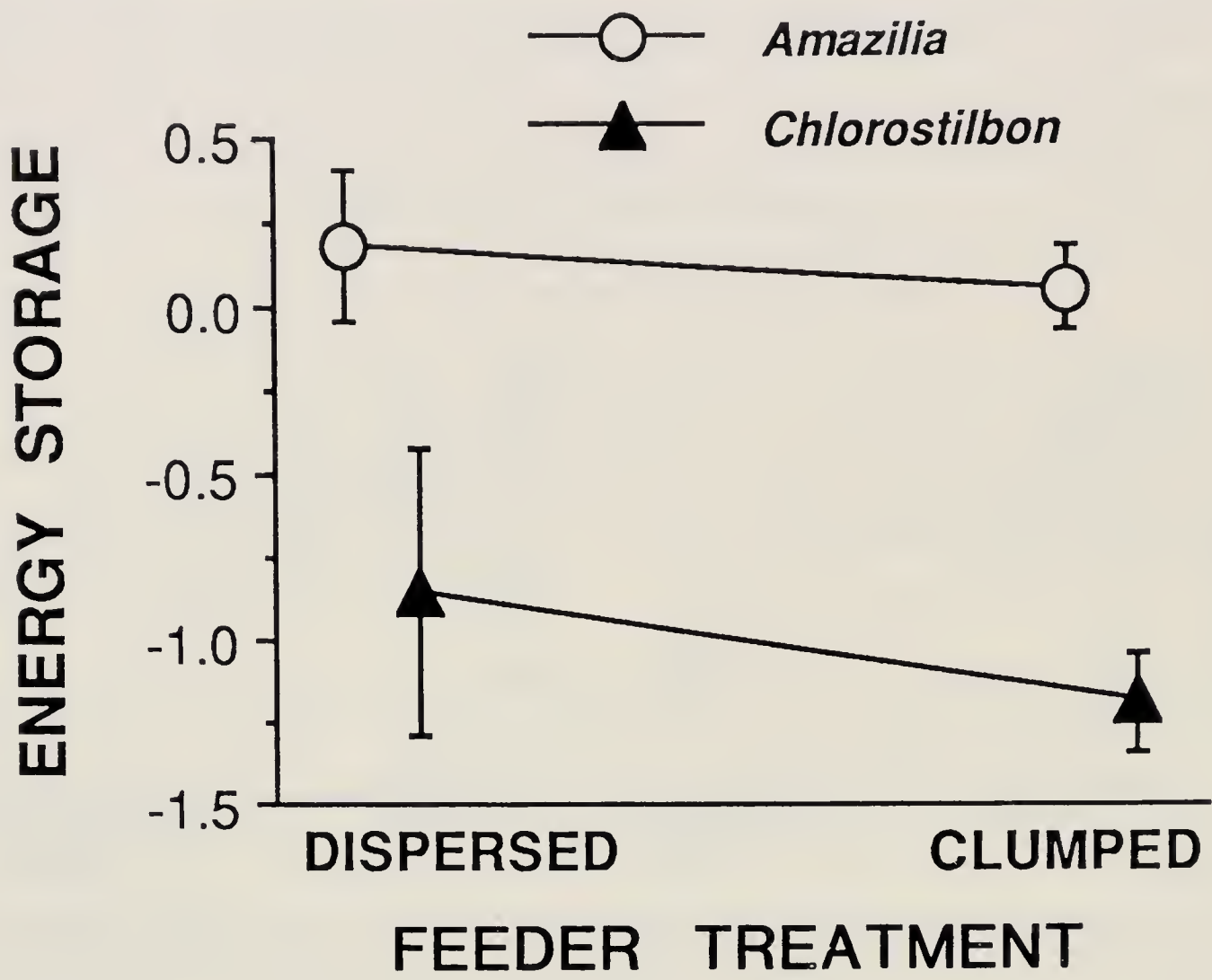


FIGURE 2 – Twenty-four-hour energy storage rates ($\text{kJ.g}^{-1} \cdot \text{d}^{-1}$) for the Steely-vented Hummingbird (*Amazilia*) and the Fork-tailed Emerald (*Chlorostilbon*) sharing limited food.

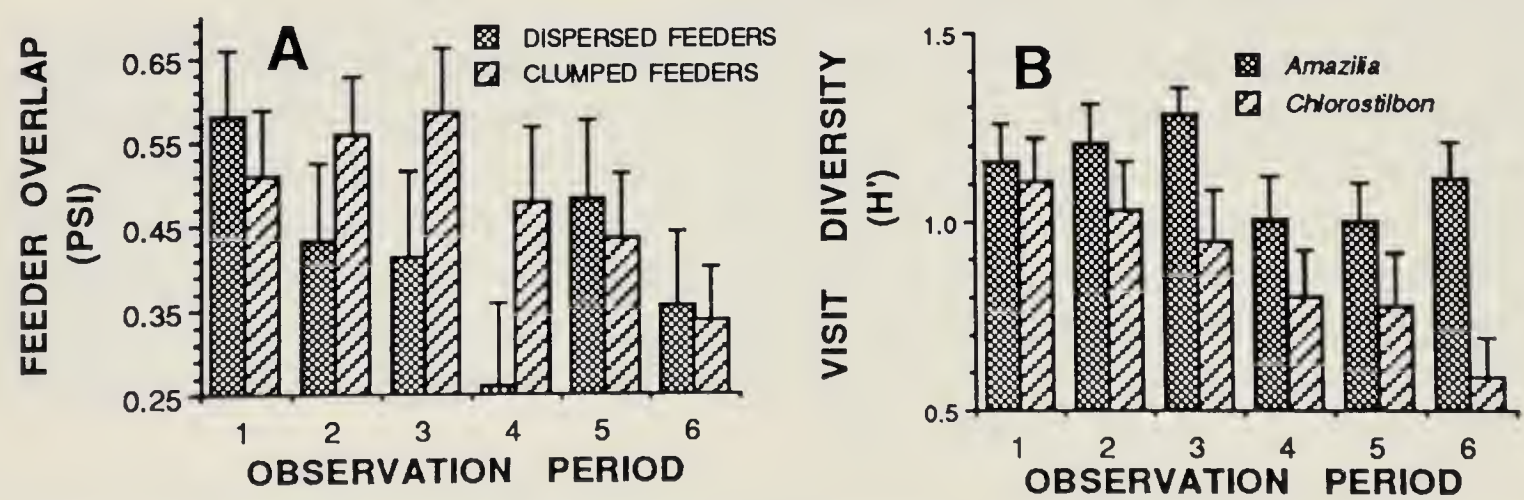


FIGURE 3 – Patterns of feeder visitation by the Steely-vented Hummingbird (*Amazilia*) and the Fork-tailed Emerald (*Chlorostilbon*). (A) Overlap in feeders visited by cagemates (PSI = Proportional Similarity Index). (B) Diversity of feeders visited (H' = Shannon-Wiener Diversity Index).

CONCLUSIONS

When food was available ad libitum, the territorial foraging mode of the Steely-vented Hummingbird proved to be a winning competitive strategy. Defending the feeder from Emeralds was energetically expensive for the territorialist, although it was just as expensive for the trapliner. The territorialist, however, had unlimited access to the feeder, whereas the trapliner did not. Emeralds were therefore unable to eat enough to compensate for the increased expenditures associated with sharing a feeder with a territorialist. This pattern may generalize to natural conditions when rich nectar

sources are clumped. As aggressive behaviour by Steely-vented Hummingbirds may force Emeralds into negative energy balance as long as trapliners remain in the patch, Emeralds should seek undefended resources if these are available. Results when feeders were clumped were similar to those for the ad libitum feeder: Emeralds maintained intake rates similar to those for Steely-vented Hummingbirds, although these were not great enough to compensate for high expenditures. Surprisingly, when limited-food feeders were widely dispersed, Emeralds were still unable to balance their energy budgets.

Emeralds generally had lower energetic success than did Steely-vented Hummingbirds. This occurred, in part, because Emeralds appear predisposed to relatively higher expenditure rates under all circumstances. These higher rates are due to the trapliners' smaller size (Lasiewski & Dawson 1967, Nagy 1987) and their tendency to fly more than Steely-vented Hummingbirds. The little trapliner thus has a much greater mass-specific energy requirement than the territorialist, and the Emerald's low-reward traplining mode may typically couple low foraging efficiency with high intake rate. My experiment, then, was artificially stacked against the Emerald. Additional foraging effort (flight time) could not be rewarded with increased intake, because food delivery was fixed at a low level. In the wild, when visiting dispersed low-reward flowers, Emeralds could compensate for low efficiency by feeding almost continuously throughout the day. Given enough flowers to visit, Emeralds should be able to forage more profitably than Steely-vented Hummingbirds because of the former's higher mass-specific intake per flower and less expensive flight.

I conclude that behavioral interactions within and between hummingbird species can have significant energetic consequences that are dependent upon ecological conditions. When two species with different foraging modes compete, they respond differentially to food availability and dispersion. This supports the hypothesis that in natural communities, hummingbird species with different foraging modes are energetically specialized for particular flower densities and/or nectar rewards. Additional research is required to establish the suggested link between energetic success in wild birds and their representation in a local nectar-feeding guild.

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COMMUNITY ORGANIZATION OF SUNBIRDS IN THE AFRO-TROPICAL REGION

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ABSTRACT. The pattern of species richness in avian nectarivores (*Nectarinia*) strongly mirrors that of birds in the Afro-tropical region in being highest in three central African refugia. Nectarivore richness does not reflect ornithophilous plant species richness in southern Africa, suggesting that the evolution of ornithophilous plants is uncoupled from that of avian nectarivores. Based on distribution patterns of ornithophily in the Cape Floristic Region, I propose that nectar production per unit plant biomass is most copious on nutrient poor soils. Patterns of dominance among sunbirds at all sites studied suggests that their community organization should be independent of plant species richness. Furthermore, with the exception of rainfall determining periods of maximum nectar flow, the only link between bird and plant community organization is that plant communities richest in ornithophilous species should support the largest avian nectarivores.

Keywords: Afro-tropics, biogeography, breeding, Cape Floristic Region, community organization, mass, nectar, foraging, *Nectarinia*, sunbirds.

BIOGEOGRAPHY OF SUNBIRDS

Fifty-eight species of *Nectarinia* (sunbirds) constitute the major component of the nectar-feeding guild in the Afro-tropical region (Collins & Paton 1989). Species richness for this genus is highest in the Central African Rift Valley, and the Cameroon and Angolan Highlands, with fewest species in the Sahara and Namib-Kalahari Deserts and in the central Congo Forests (Figure 1). This pattern mirrors that of both Afro-tropical passerine and nonpasserine bird species (Crowe & Crowe 1982). Furthermore, Afro-tropical *Nectarinia* species richness is significantly positively correlated ($r=0.66$, stepwise regression analysis) with vegetation diversity ($R^2 = 0.22$) and the range of monthly rainfall ($R^2 = 0.03$), and negatively with mean maximum temperature ($R^2 = 0.12$) and mean annual temperature ($R^2 = 0.14$). These are similar to those results obtained for total passerine species richness (see Crowe & Crowe 1982 for methods and environmental variables considered).

This suggests that geographical patterns of speciation and niche packing in *Nectarinia* are no different from those of other avian guilds, despite the possibility of near species-specific coevolution between plants and nectarivores (Snow & Snow 1980). Tropical forest trees, mammals, butterflies and amphibians exhibit the same patterns of species richness and endemism as birds. On this basis, Diamond & Hamilton (1980) proposed that three high-altitude forest refugia existed during arid Quaternary times. They suggest that competitive exclusion may be partly responsible for the apparent lack of species colonization outside of refugia.

Mean *Nectarinia* body mass (mean of all species per grid square) is relatively constant at 10.3 g, irrespective of species richness for the Southern Savanna / South-west Arid Subregion (Figure 1). Within the Forest Subregion, mean mass is constant relative to

species richness above 15 species, but increases with lower species richness. By contrast, mean body mass decreases markedly with lower species richness in the Sahara / Northern Savanna / Northeast Arid Subregion (Figure 1), a trend which continues northwards with a single 5 g species in Israel (Eisikowitch & Nahari 1982). This pattern occurs because heavier *Nectarinia* species drop out preferentially in species-poor assemblages. The reverse is true in Forest and Southern Savanna and desert, where lighter species drop out. Furthermore, there is a tendency for the heaviest species to persist in the extreme south of the Southern Savanna Subregion: this pattern is consistent with, and in spite of, the presence of two much heavier nectarivorous bird species (*Promerops* spp: 38 g) in the region (Rebelo 1987). These geographical patterns in body mass are paralleled by bill length (unpublished data).

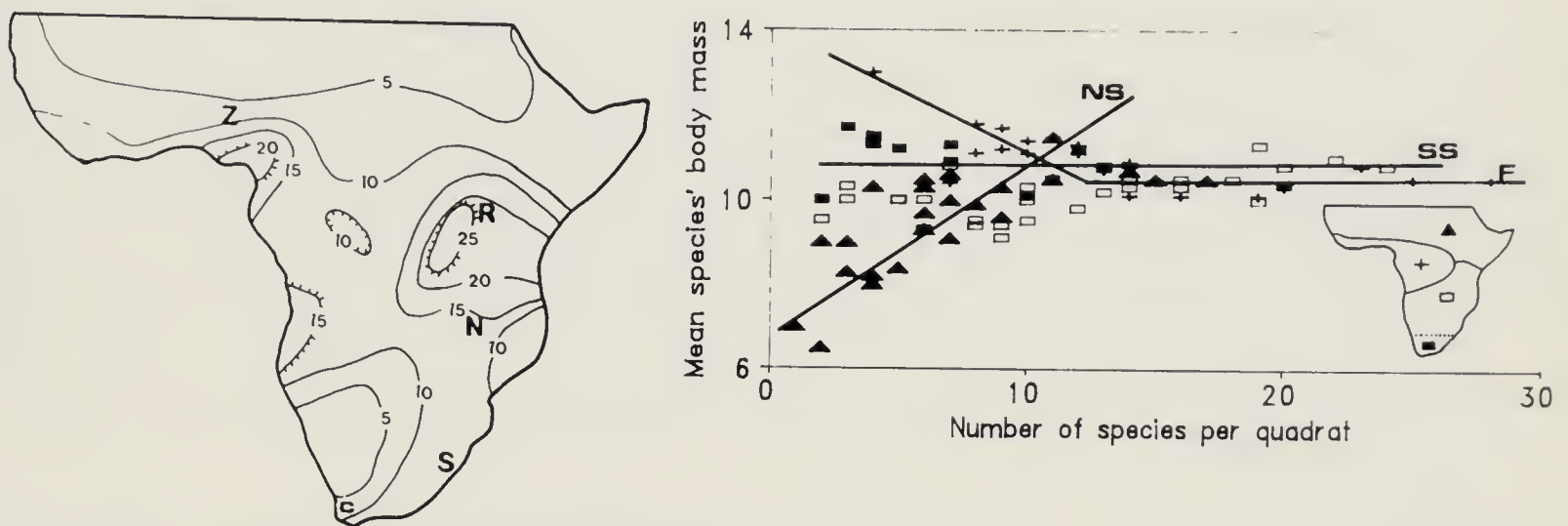


FIGURE 1 – (Left) Geographical variation in *Nectarinia* species richness in the Afro-tropical Region. Data from Hall & Moreau (1970); see Crowe & Crowe (1982) for methods. Letters indicate regions discussed in text (C- Cape Floristic Region; N-Nyika Plateau; R- Rift Valley; S- Zululand; Z-Zaria). (Right) The relationship between the number of species per area (4° quadrat) and mean body mass of species for different biogeographical subregions in the Afro-tropical Region (Forest (F) + ; Northern Savanna & Arid (NS) \blacktriangle ; Southern Savanna & Arid (SS) \square , with \blacksquare denoting the southern-most quadrats). Body mass is the mean for the species, irrespective of any geographical variation in mass. Data as for Figure 1 (left) and Rebelo (unpublished data).

COMMUNITY ORGANIZATION

Few accounts of community organization of Afro-tropical avian nectarivores at specific sites over an annual cycle exist. These are for: Coastal Dune Forest in Zululand (Frost 1977, Frost & Frost 1980); Nyika Plateau in Malawi (Dowsett-Lemaire 1989), Zaria in Nigeria (Pettet 1977); the highlands of the Rift Valley in Kenya (Chapin 1959, Cheke 1971, Cunningham van Someren & Miskell 1976, Wolf & Wolf 1976, Gill & Conway 1979, Wolf & Gill 1986); and the Cape Floristic Region (CFR: Collins 1983, Rebelo et al. 1984, Siegfried & Rebelo 1988, Rebelo 1987, Fraser et al. 1989, Underhill & Fraser 1989). A brief summary of the organization of these communities is available on request. However, data on patterns of ornithophilous plant community organization are available only for the CFR (Rebelo 1987, Rebelo & Jarman 1987), and allow a comparison of plant-sunbird interaction at the community level.

Ornithophilous plants in the Cape Floristic Region

Species richness of avian nectarivores decreases with increasing latitude (Figure 1), despite the presence of the Cape Floristic Region (CFR) in the south. The CFR contains over one-third of southern Africa's plant species and 75% of its ornithophilous species (Rebelo 1987). It is exceptionally rich in plant species, with high levels of endemism equivalent to the richest centres of endemism in tropical rain-forests (Cowling et al. in press).

The CFR comprises five major vegetation types: Fynbos (roughly equivalent in structure to the Proteaceous-Ericaceous Moorland of the Afro-tropics) on nutrient-poor sandy soils, and Afro-montane Forest, Karee, Renosterveld and Thicket on nutrient-rich soils, the last three being confined to the lowlands (Rebelo & Jarman 1987). Fynbos soils are poor in nitrogen, phosphorus and potassium. Low levels of these elements limit plant protein synthesis, allowing excess carbohydrates to be allocated to sclerophylly and reproduction, specifically in the form of large flowers and nectar (see Rebelo & Jarman 1987). Thus, although primary production in Fynbos is low, nectarivores comprise a mean of 50% of avian biomass in mature Mountain Fynbos over an annual cycle (Siegfried 1983). By contrast, nectarivores comprise less than 3% of the mean annual avian biomass of vegetation communities on Renosterveld and Thicket, and on Lowland Fynbos of the west coast, which supports half the total standing crop biomass of avian nectarivores in Mountain Fynbos (Siegfried 1983).

The flowering phenology of ornithophilous plant species is affected by rainfall patterns. On mountain slopes, species flower mainly during the winter rains. Spring-summer flowering species occur chiefly at high altitudes, sustained by mist precipitation from south-easterly clouds, or in low altitude seeps, where plant activity is restricted by water-logging in winter (Rebelo et al. 1984, Rebelo 1987). Similarly, most succulent Karoo ornithophilous species flower during winter / spring (Rebelo 1987). The genus *Leucospermum* (Proteaceae) is restricted to flowering in spring, apparently because of its myrmecochorous seed-dispersal syndrome (Collins & Rebelo 1989). On the south coast lowlands, where rainfall peaks in autumn and spring, a group of ornithophilous species (section *Tumiditubus*) occurs, whereas the winter rainfall region of the west coast lowlands supports an entomophilous section (*Leucospermum*) (Rourke 1972). This may be linked to the absence of *Nectarinia violacea* in Fynbos vegetation from only the lowlands of the west coast (Rebelo 1987).

The Proteaceae, Ericaceae, Iridaceae and Asphodelaceae comprise over two-thirds of the bird-pollinated plant species in the CFR. Only the last-mentioned family is not restricted mainly to Fynbos vegetation (Rebelo 1987). High avian nectarivore biomass (chiefly *N. violacea* and *Promerops cafer*) is largely confined to mature vegetation, with very few birds present before re-seeding species have flowered, i.e. at about four years post-fire (Fraser 1989). Although re-sprouting plant species do occur, they are usually sparsely distributed (unpublished data), with the exception of geophytes, which attract mainly *N. famosa* (Rebelo 1987). In Thicket vegetation, bird-pollinated plant species (Amaryllidaceae, Lamiaceae, Solanaceae) are mainly confined to the early seral stages, whereas in Renosterveld ornithophilous species are largely confined to geophytes and in Karoo vegetation to succulents (Asphodelaceae, Crassulaceae) (Rebelo & Jarman 1987).

Patterns of avian nectarivore community organization in the Afro-tropics

Patterns of sunbird community organization and ornithophilous plant distribution and phenology in the CFR are consistent with that found in the rest of Africa. Briefly, in almost all sunbird assemblages studied, the species composition at a resource is determined by the heaviest species. Heaviest species exploit only the richest resources, and their breeding cycle is determined by the availability of uncontested, high-nectar flows. However, when nectar resources are over-abundant, non-antagonistic feeding by all local species may occur. By contrast, when nectar is in short supply, territorial birds swamped by flocks of the same or smaller species may abandon territorial behaviour and resort to rapid exploitative feeding within their territory. Largest species are also the most itinerant, as they have the highest resource requirements, which are unlikely to be met continuously.

Smaller nectarivore species are excluded from the richer nectar resources for much of the annual cycle. These smaller species feed off a very wide nectar-resource base, including entomophilous plant species, and extensively thief nectar illegitimately from long-tubed ornithophilous species. In all areas studied, breeding of smaller nectarivore species is tied to heavy utilization of insects, and breeding territories often contain no flowers.

Intermediate-sized bird species are often the most resident species in a community, with smaller species being excluded during poorer nectar flows and larger species present only at the richest nectar flows.

Only male sunbirds and sugarbirds defend territories during the breeding season (Skead 1967). Males are monogamous and females nest within their territories, participating in territorial defence (except during incubation), especially against females. During the non-breeding season, both male and female sugarbirds defend feeding territories (Rebello 1987). In sunbird species, it appears that pairs occasionally defend feeding territories outside of the breeding season, but more often individual feeding territories are defended or birds join mobile feeding flocks (Skead 1967). Although data are very scanty, it appears that in larger species females defend feeding territories, whereas in smaller species they join feeding flocks. The relationship between bird size, sexual dimorphism and patterns of territorial resource utilization outside of the breeding season requires investigation, especially with regard to species having eclipse plumage in the males (Skead 1967).

Thus avian nectarivore communities in the Afro-tropics are very similar to those of the neotropical hummingbird-diglossid (Snow & Snow 1980, Stiles 1981) and Australian honeyeater communities (Collins & Newland 1986, Paton 1986a). The major difference between sunbird and honeyeater versus hummingbird communities is the presence of high quality trapliners in the latter (B.G. Collins pers. comm., Snow & Snow 1980). Because sunbirds require perches for nectar feeding, smaller birds can pierce and thief from long-tubed ornithophilous flowers, thus gaining access to undefended 'specialized' resources. Hummingbird-pollinated species with distal flowers on thin stalks (unavailable to perching diglossids) cannot be thieved. Consequently, nectar resources in long-tubed species accumulate, allowing traplining. Thus, subordinate sunbirds (including females) with shorter bills can thief unprotected nectar, and long bills on small birds is not a stable strategy. However, longer bills on subordinate species and female hummingbirds (Paton & Collins 1989) allow these birds to trapline unexploited flowers which are unavailable to perching diglossids.

SYNTHESIS: TOWARDS A MODEL OF THE ORGANIZATION OF NECTARIVORE-ORNITHOPHILY IN COMMUNITIES

Plant communities

Evidence that entomophilous plant species produce less nectar energy or water per plant than related ornithophilous species is lacking (Evenson 1983), although such a phenomenon seems likely. Nevertheless, net energy and water cost per seed produced is probably many times higher for the larger-flowered ornithophilous species than for closely related entomophilous or anemophilous species in the same habitat (Stiles 1978). Therefore, ornithophilous species should predominate in areas where excess water and energy are available (Rebelo & Jarman 1987). Systems in which excess energy is present exist on highly-leached soils, especially those poor in nitrogen, potassium and phosphorus, typical of high rainfall areas and sandy substrata, and characterized by sclerophyllous and moorland vegetation (Rebelo & Jarman 1987). For similar reasons, epiphytes and lithophytes should also be ornithophilous in high rainfall areas. Arboreal hemi-parasites on trees, restricted from growing too large by physical constraints, may also have excess energy for reproduction. Early seral plant species, which invest proportionally more of their resources in reproduction, may generate surplus energy if nutrient availability limits seed production.

In areas where nitrogen and other minerals are more readily available, plants should channel energy into growth, at least until they have established a competitive advantage. Mature plants in these communities will benefit by channelling energy into propagules. Ornithophily should be scarce in these environments.

The production of copious, dilute nectar is dependent upon adequate water, although deep-rooted species can produce such nectar well into the dry season. Individual trees with access to abundant water may produce more copious nectar than water-stressed neighbours (Pettet 1977). Arboreal hemi-parasites on trees should have access to abundant water, especially those species flowering during the leafless stage of their deciduous host plant species.

Thus, it should be possible to develop a model to predict the probable incidence and phenology of ornithophily in plant communities, given climatic, topographic and soil conditions at any site. Predictions based on the above considerations include: within any landscape the most nutrient-poor soils should support the highest biomass of avian nectarivores. The extremely nutrient-poor soils within SW Australia should have some of the highest nectar flows (per plant biomass and per hectare), and support the highest biomass of avian nectarivores worldwide; the incidence of ornithophily should increase with increasing rainfall and altitude, both because of higher water availability and greater leaching of soils; flowering phenology of ornithophilous species should be significantly more constrained to periods of high water availability (not necessarily rainfall) than that of other pollination syndromes, with the exception of waterlogged and flooded sites, which may only start producing nectar once root activity commences. Thus, Mediterranean regions should have a flowering peak of ornithophilous species in winter, as opposed to other neighbouring climatic regions, whereas entomophilous species should be less restricted by periods of rainfall and more by insect abundance; and water-storing ornithophilous plant species (bromeliads and succulents) may flower later than most other plant guilds.

During the past two million years, vegetation changes appear to have occurred on a large scale in Africa (Diamond & Hamilton 1980). Species present in an area comprise those which locally survived the previous climatic changes, those which evolved in situ, and those which colonized the area during the current climatic conditions. This does not imply that species currently occupy optimal habitats. Populations of maladapted species may be sustained by excess seed production from neighbouring suitable habitats. Similarly, niche expansion may restrict further invasion or in situ evolution (Diamond & Hamilton 1980). For plants, this suggests that many possible niches may be locally vacant. Assemblages may consist of temporary associations of species with independent migration patterns (Feinsinger 1987a). It is in refugia, therefore, that predicted niches have the highest probability of being realized (Feinsinger 1976). Given the current rate of ecosystem transformation in the tropics, it is imperative that these systems be studied as soon as possible (Feinsinger 1987b).

Bird communities

Intuitively, it appears simple to model avian nectarivore community composition. Relevant factors influencing the presence of a species at a site include: inherent habitat preferences (especially for roosting and nesting), nectar resources (quantity, quality, dispersion), protein resources (relatively insignificant), and local densities of other avian nectarivores.

The overall abundance of sunbirds in a region is a function of the seasonal minimum nectar resource and the amount of emigration and immigration. Where the nectar resource is relatively constant throughout the year, most species should be resident. Larger species ("organizers") should enter the system when more profitable species outside the region stop flowering, and smaller species when more profitable species outside start flowering.

Thus, modelling sunbird communities probably poses the same problems faced by individual sunbirds (Wolf & Hainsworth 1983). Where are the best resources and how far must birds travel to get to them? Which bigger sunbird species are likely to visit and dominate the resource? Unfortunately, there are inadequate data on distances moved by sunbirds to resolve these questions. Even on an annual scale, stochastic climatic variation, perturbations resulting in secondary growth that are unpredictable locally and temporally, fluctuating plant densities, and neighbouring sites subjected to different climates and perturbations prevent the evolution of specific plant sunbird associations and determine the scale of bird movements (Wolf & Gill 1980). Thieving by smaller species from undefended long-tubed corollas specifically restricts the evolution of traplining with the result that female sunbirds must defend feeding territories or join flocks outside of the breeding season.

Ideally, a model of local sunbird community assembly, coupled with resource densities, should be able to predict regional species richness. But inherent habitat preferences seem to play a major role in determining the distribution of nectarivorous species. No rules governing the number of nectarivore (or ornithophilous plant) species on a local scale are apparent. Bird species that are especially efficient at exploiting a resource may be displaced by larger, less efficient species. Thus, although the regional pattern of sunbird species richness appears to mirror that of other bird taxa, and may reflect species habitat preferences, at the local level individual sunbird behaviour may be sufficiently flexible to generate considerable "noise", especially where

different habitats co-exist. Why, for instance do *N. violacea*, *Nectarinia fusca*, and *Nectarinia chalybea*, each roughly with a mass of 8-10 g, wing length of 47-58 mm and culmen length of 18-23 mm, replace one another in Fynbos, Karoo and Renosterveld / Thicket vegetation, respectively (Rebelo 1987)?

Currently intractable questions that should be addressed in order to model the dynamics of sunbird communities include: Why have sunbird species not dispersed from the putative refugia? Since there is a strong correlation between species richness and vegetation diversity, are species-rich areas actually refugia or areas where the high diversity of vegetation types are particularly finely partitioned by species? Does the presence of only small sunbirds in the Sahel region of the Sahara indicate that desertification is reducing the nectar output of ornithophilous plant species in the region? Are ornithophilous plant species especially sensitive to desertification?

Although speculative, the above discussion outlines several shortcomings of studies of nectarivore-plant community organization. With emphasis on inflorescences and flowers, plants as units producing nectar have been ignored. Most studies encompass a range of habitats and seral stages within a locality, and provide average rainfall data of no relevance to the period of study. Considerable information is thereby lost.

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CONCLUDING REMARKS: SOCIAL PATTERNS IN NECTARIVOROUS BIRDS

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INTRODUCTION

Several interesting patterns have emerged from this symposium. The following discussion will draw primarily from the studies presented today. However, I also will mention a few previous investigations in appropriate places. I have made no effort to review the literature, as space is limiting.

The single most important underlying pattern is that the food source of nectarivorous birds shares many of the same traits in all communities. The availability of floral nectar changes both spatially and temporally. Yet, because flowers are non-mobile, conspicuous, and usually productive for a period of days to weeks, they are potentially defensible. The fact that the nectar of an area may be exploited rapidly if it is not defended encourages many nectarivorous birds to be aggressive and defend solitary, pair, or group territories.

When different areas flower at different times, nectarivores must be nomadic or even migratory, and this resource variability seems to preclude cooperative or colonial behaviour (McFarland & Ford this symposium). There seems to be no necessary connection between degree of nomadism and degree of aggressiveness. In the African system (Rebelo this symposium), the resident species were dominant to the migratory species. However, migratory species within the Australian honeyeaters (McFarland & Ford this symposium) and New World hummingbirds (Wolf et al. 1976) are sometimes dominant to less migratory or resident species.

BODY SIZE AND WING-LOADING

So what determines aggressive dominance in these birds? Two factors seem to be important, depending on the system: body size and wing-loading, the ratio of body mass to wing area (Collins & Paton 1989). The Australian honeyeater species studied varied greatly (six-fold) in body size (Collins & McNee this symposium) and the species in these communities may vary much more than that. The hummingbirds studied varied much less (Tiebout this symposium). In fact, only about a two-fold difference exists among all the common hummingbird species in the United States, although a greater size range (6- to 10-fold) does occur in the New World tropics.

When a large range in body size occurs in a community, aggressive dominance seems to be related largely to body size: the larger the species, the more dominant they are. Thus, the Little Wattle Bird and Yellow-throated Miner were able to exploit

the richest resources (Collins & McNee this symposium), presumably through behavioural aggression (McFarland & Ford, this symposium). Similarly, dominance hierarchies among the moderately size-differentiated hummingbirds of Central America are to some extent determined by size (Wolf et al. 1976), but wing-loading also plays a role (Colwell 1973, Feinsinger & Chaplin 1975, Tiebout this symposium).

When coexisting species do not vary much in size, differences in wing-loading alone may be associated with differences in aggressive dominance. Higher wing-loading is thought to confer advantages in agility and therefore territorial defense, but at the cost of more expensive flight (Feinsinger & Chaplin 1975). These differences occur not only among species in hummingbird communities (Colwell 1973, Tiebout this symposium), but also between sexes within a single species (Kodric-Brown & Brown 1978, Carpenter et al. this symposium). The lower wing-loaded species or sex is either non-territorial (Tiebout, this symposium) or territorially disadvantaged (Carpenter et al. this symposium) relative to higher wing-loaded birds.

ENERGETICS

In all the studies discussed in this symposium, subordinates were smaller and/or lower wing-loaded than dominants. The former should have reduced rates of total energy consumption, *given the same activity level* as birds with larger bodies or higher wing-loading. One would expect, then, that the subordinate sex or species would be able to maintain itself energetically on nectar sources that are distributed more sparsely or are less productive per flower. This in turn, however, would increase their activity level since more flowers must be visited or greater distances flown. The question is whether the energetics balance.

By means of energetic calculations, Collins & McNee (this symposium) showed that the energetics of the small-bodied Western Spinebill did balance. However, when Carpenter et al. (this symposium) and Tiebout (this symposium) performed controlled experiments and measured net energy gain directly by monitoring changes in body mass, they obtained equivocal results. Although the subordinate sex/age class of Rufous Hummingbirds eventually gained enough mass to resume migration, some data suggested that these birds may have been disadvantaged relative to the dominant males (Carpenter et al. this symposium). Under Tiebout's experimental conditions, the subordinate hummingbird species could not maintain positive energy balance, whereas the territorial dominant could. More data are needed to resolve the question of whether small and/or low wing-loaded subordinates compensate for being excluded from the richest resources by having cheap, efficient foraging behaviour. Common sense suggests that they must.

SUBORDINATES AND NICHE REFUGES

In terms of niche theory, we may describe our systems as communities exhibiting included niches (Colwell & Fuentes 1975). If resources are limited and competition is important, a species whose niche is included within that of another must be competitively dominant within its specialized niche. The more generalized species, on the other hand, may prefer the same resources used by the specialized dominants. If excluded from them, however, it can take refuge within the other portion of its niche.

We often see in nectarivorous bird communities that subordinates are not only small and/or low wing-loaded, and use poorer nectar sources, but also may be quite generalized. This pattern was reported in this symposium for Australian honeyeaters (Collins & McNee), African nectarivores (Rebelo), and New World tropical hummingbirds (Tiebout), and has also been noted in Hawaiian Honeycreepers (Carpenter & MacMillen 1980).

Subordinates survive, therefore, in several ways. They may exploit plant species that are less productive than those used by dominants (Collins & McNee this symposium, Rebelo this symposium, Feinsinger 1976). They may exploit patches of more sparsely distributed flowers within the same plant population used by dominants (e.g. Rufous Hummingbird immature females, Carpenter et al. this symposium, Central American traplining hummingbirds, Feinsinger 1976 and Tiebout, this symposium, Hawaiian honeycreepers, Carpenter & MacMillen 1980). Or, they may even exploit the same patches of the same floral species, but concentrate on less productive flower stages that are ignored by dominants (Collins & McNee this symposium). Thus, low-producing floral species, sparsely-flowering patches and/or low-producing age classes of flowers are all refuges for subordinates, which may prefer but be excluded from richer resources.

TURNING TERRITORIALITY ON AND OFF

Another pattern that emerged from this symposium, in conjunction with previous studies, was that a single species may show flexible behaviour, ranging from solitary to colonial and from territorial to cooperative. Territoriality, in particular, has been shown to turn on or off depending on resource availability. This phenomenon is demonstrated by Australian honeyeaters (McFarland & Ford this symposium), New Zealand Tuis (Stewart & Craig 1985), Hawaiian honeycreepers (Carpenter & MacMillen 1976), and even the notoriously aggressive Rufous Hummingbird (Carpenter 1987). In all these nectarivorous birds, as well as in totally different groups such as aquatic insects (Hart 1987), territoriality occurs at intermediate levels of resource availability, disappearing when resources are regionally either very scarce or superabundant.

Territoriality may also disappear when resources are extremely clumped locally, so that defence may be swamped by large numbers of invaders (Myers et al. 1981). In enough numbers, subordinate species may even swamp defence by dominant species (McFarland & Ford this symposium).

FUTURE DIRECTIONS

This symposium suggests several questions that should be addressed in future research:

1. Can we demonstrate that the energy savings of low wing-loading and/or small body size compensates subordinates for their forced use of poor nectar sources?
2. How would high wing-loaded birds fare energetically if forced to trapline very dispersed flowers?

3. Could wing-loading (as well as body size) help explain why some species of Australian honeyeaters are more territorial than others? Do interstitial species such as the Yellow-faced Honeyeater mentioned by McFarland & Ford (this symposium) have low wing-loading (as well as small size) which helps reduce energy costs? Is the extreme flexibility of behaviour in the New Holland Honeyeater permitted by an intermediate level of wing-loading, given its body size? If its wing-loading is too high, the species would be inefficient when food is dispersed and territories not feasible, but too low a wing-loading might prevent it from ever being territorial. Species that overlap in resource use and are similar in body size could be measured to see if there are patterns in wing-loading and relative dominance.
4. In the absence of territorialists, how would trapliners react to clumped, rich nectar? Would they defend intraspecific territories? Or establish dominance hierarchies? This question could be answered by experimental manipulation of floral resources and removal of species known to be territorial.

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SYMPOSIUM 19

**SOCIAL BEHAVIOUR IN THE
NON-BREEDING SEASON**

Conveners S. YAMAGISHI and J. KIKKAWA

SYMPOSIUM 19

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INTRODUCTORY REMARKS: SOCIAL BEHAVIOUR IN THE NON-BREEDING SEASON

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It is appropriate to discuss behavioural ecology in terms of 'fitness'. Because fitness is often measured directly as breeding success, ornithologists studied only the breeding season and its immediate past and future for this purpose. It is now recognised that the fitness measured in a single breeding season is inadequate and that life-time reproductive success is considered important in assessing the fitness in the light of natural selection. However, when life-time reproductive success is considered fitness is a measure of the result of complex interactions among many factors, yet not much attention was paid to the important relationship between the social behaviour of the non-breeding season and that of the breeding season. Does social behaviour of the non-breeding season contribute to breeding success of the individuals concerned? If so, what processes and mechanisms have been subject to natural selection? This symposium on "Social behaviour in the non-breeding season" is to elucidate the role of natural selection in moulding such behaviour.

COMPARISON OF BREEDING SUCCESS BETWEEN RESIDENTS AND IMMIGRANTS IN THE GREAT TIT

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ABSTRACT. Great Tits *Parus major* of Sagamihara, Japan, formed flocks of constant composition with overlapping flock ranges in the non-breeding season. In the breeding season, most surviving males paired with females of the same flock and established territories within their own flock ranges. On the other hand, immigrants which did not belong to any flock in the study area emigrated from the surrounding area and settled in the vacant space of flock ranges. So the breeding population consisted of these two groups of birds with different previous history. Comparing breeding success between the resident flocks and the immigrant pairs, the former raised more surviving young than the latter. Familiarity with the future breeding area seems to bring about high breeding success.

Keywords: Great Tit, breeding success, residents, immigrants, familiarity with breeding area.

INTRODUCTION

The breeding biology of the Great Tit *Parus major* has been studied intensively since Kluijver's study (1951) was published. It is well known that breeding success varies with environmental factors, population density, characteristics of the birds themselves and pair bond during the breeding season. However, breeding success has not been discussed in relation to non-breeding biology.

In the non-breeding season, most Great Tits settle in particular areas during their first autumn and stay there for the rest of their life (Kluijver 1951, Saitou 1979b). They form flocks of constant composition with overlapping flock ranges (Saitou 1978, 1979a, b, 1988). In the following spring, flock members usually pair with other members of the same flock and establish their territories within their own flock ranges (Saitou 1979c). These residents breed within areas familiar throughout the previous winter. If the residents could increase their chances of raising young by breeding in familiar areas, familiarity with the future breeding area would be an important factor for breeding success. In this paper, I compare breeding success between residents and immigrants which breed in unfamiliar areas, and discuss the effect of familiarity with the future breeding area on breeding success.

STUDY AREA AND METHODS

The study was conducted at a golf course in Sagamihara, Kanagawa, Japan. Out of 160 ha occupied by the golf course, 70 ha was a mixed woodland consisting of conifer trees, *Pinus densiflora*, *Cryptomeris japonica*, *Chamaecyparys pisifera*, and deciduous broad-leaved trees, *Quercus acutissima* and *Q. serrata*. The woodland was located between fairways of the course, and was open and narrow, 60 m across at its widest. The ground was maintained as part of golf course management.

There were only few natural tree holes suitable for breeding or roosting. I provided nesting boxes throughout the year and roosting boxes, a quarter size of nesting boxes in volume, during the autumn and winter.

All adults that bred in the nesting boxes and their young were marked individually. Some birds immigrated into the study area from the surrounding areas. Such birds were captured with mist-nets, in the roosting boxes during the autumn and winter or at the nesting boxes in the breeding season, and were marked. The individual history of each marked bird was recorded, so their previous histories were known.

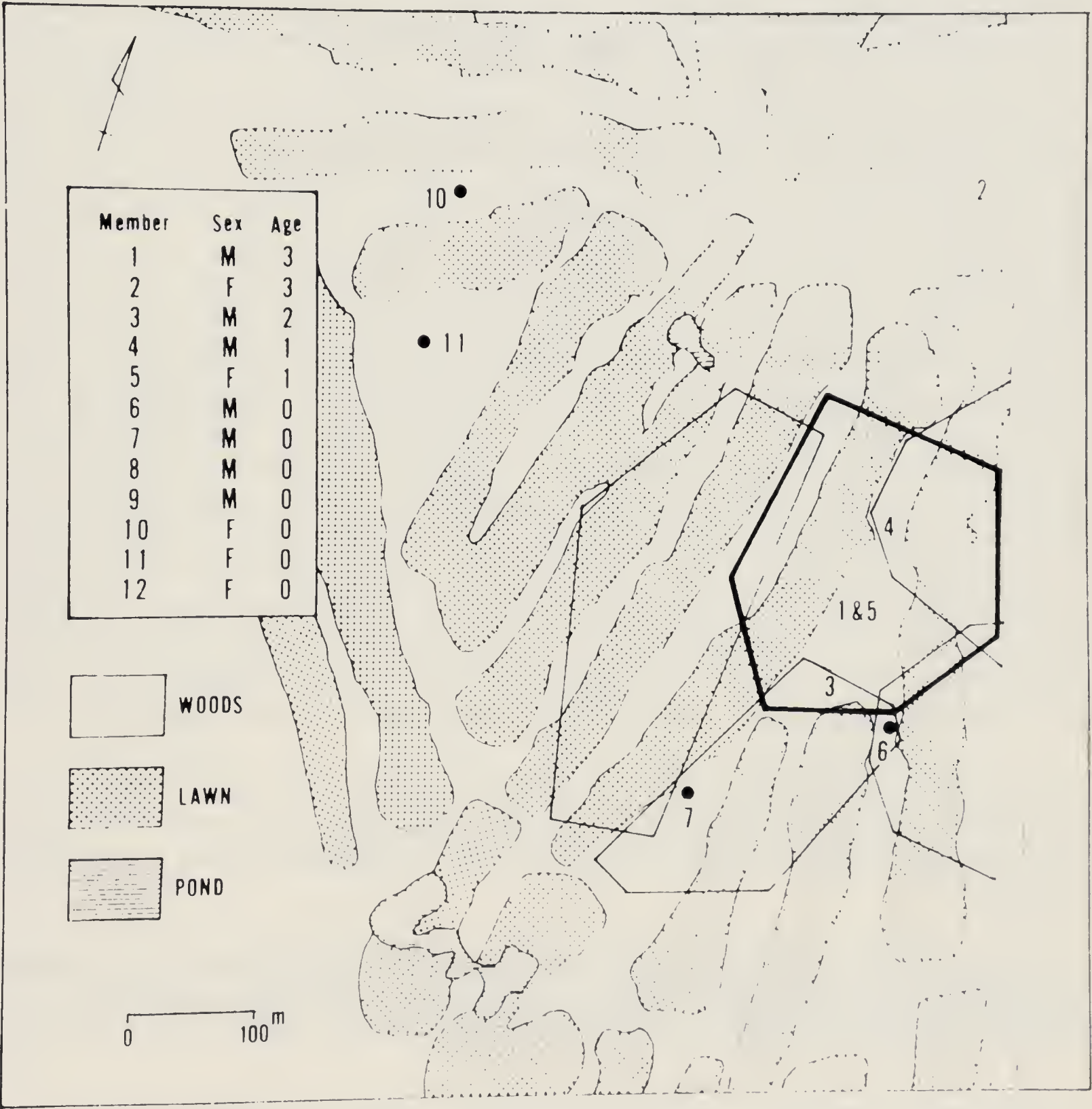


FIGURE 1 - A list of flock members, flock ranges and breeding sites or birth places of members. M, male. F, female. Polygon, flock range. Open circle, breeding site of old bird. Black circle, birth place of young bird. Members 8, 9 and 12 were immigrants in autumn. Members 1 and 5 were a breeding pair in 1986. Member 2 had belonged to this flock in 1985-86 and emigrated to breed in other area, but returned to previous flock range in 1986-87.

During the autumn and winter, each flock was observed at least once a week for 10 minutes to an hour at a time, depending on the number of birds forming the flock. The nesting and roosting boxes were visited once in early December and again in early March, and all the roosting birds were checked.

In the breeding season, all nests were visited once every three days and the breeding results were recorded. The analysis was based primarily on an examination of the fledging success of 354 first brooded nests during four years 1985-1988. All nests in this sample satisfied two criteria; every nest had at least one young to leave the nest, and the previous histories of both parents were known. I examined four parameters: (a) the date of laying (laying dates are based on the first egg laid in each nest and are scored from 1 April = 1); (b) the clutch-size; (c) the number of young that fledged; (d) the number of young that survived at least three months after leaving the nest. All four parameters varied from year to year. In order to eliminate the year effect, I standardized all the data by computing the z-score (Perrins & McCleery 1985) for all nests, and t-tests were used in statistical comparisons. Breeding birds are divided into two large groups according to familiarity with the breeding area: residents and immigrants. The residents are the flock members that remain and breed in their own or neighboring flock ranges which overlap with their own. They have familiarized themselves with these throughout the preceding autumn and winter. The immigrants consist of three groups: those that emigrate from their flock ranges and breed in ranges of other flocks which do not overlap with their own; those that immigrate into the study area from the surrounding areas in spring; and those that have bred in the study area the year before, but wintered elsewhere only to return to the study area in the following spring. The last group of birds are subdivided into two types according to whether the bird was familiar with the breeding area. Type A is those birds that bred in or near their previous breeding area. Type B is those that bred at new sites within the study area but far from their previous breeding area. While the first two groups of birds and type B migrants were unfamiliar with their new breeding area, type A migrants bred in their familiar breeding area. Therefore, there were three groups of breeding pairs, RR, RI and II, where R and I represented resident and immigrant respectively.

Ages were divided into two categories: young (Y = one year old) and old (O = aged two or older). There were therefore four age-sex combinations of breeding pairs OMOF, OMYF, YMOF and YMYF, where M and F represented male and female respectively.

The following sketch summarizes the characteristics of winter flocks with an example of a flock formed in the winter of 1986-87 in the study area, and presents background information about the residents and the immigrants.

The flocks were constant in membership (Saitou 1978). As shown in Figure 1, the flocks did not have any particular sex composition or any preferred age composition. Most flocks consisted of one previous breeding pair and young that were not related to the pair by blood. The flock ranges were well-defined and based on the previous territories of adults belonging to the flock (Saitou 1979b). A flock range overlapped with those of neighboring flocks (Figure 1) and the flock members selected their roosting sites within their flock ranges. The flocks usually moved about their flock ranges by themselves, but the neighboring flocks joined frequently to form compound flocks in mid-winter (Saitou 1978, 1982). The compound flocks foraged over all or some of the flock ranges of joined flocks and eventually broke up into individual flocks.

The flocks eventually broke up by early March. The pair formation took place during or after the break-up of the flocks. Most flock members established territories within their flock ranges (Figure 2). Some members emigrated and bred in other ranges which did not overlap with their own. Also, some birds immigrated into the study area from surrounding areas and held their territories in the vacant space of flock ranges.

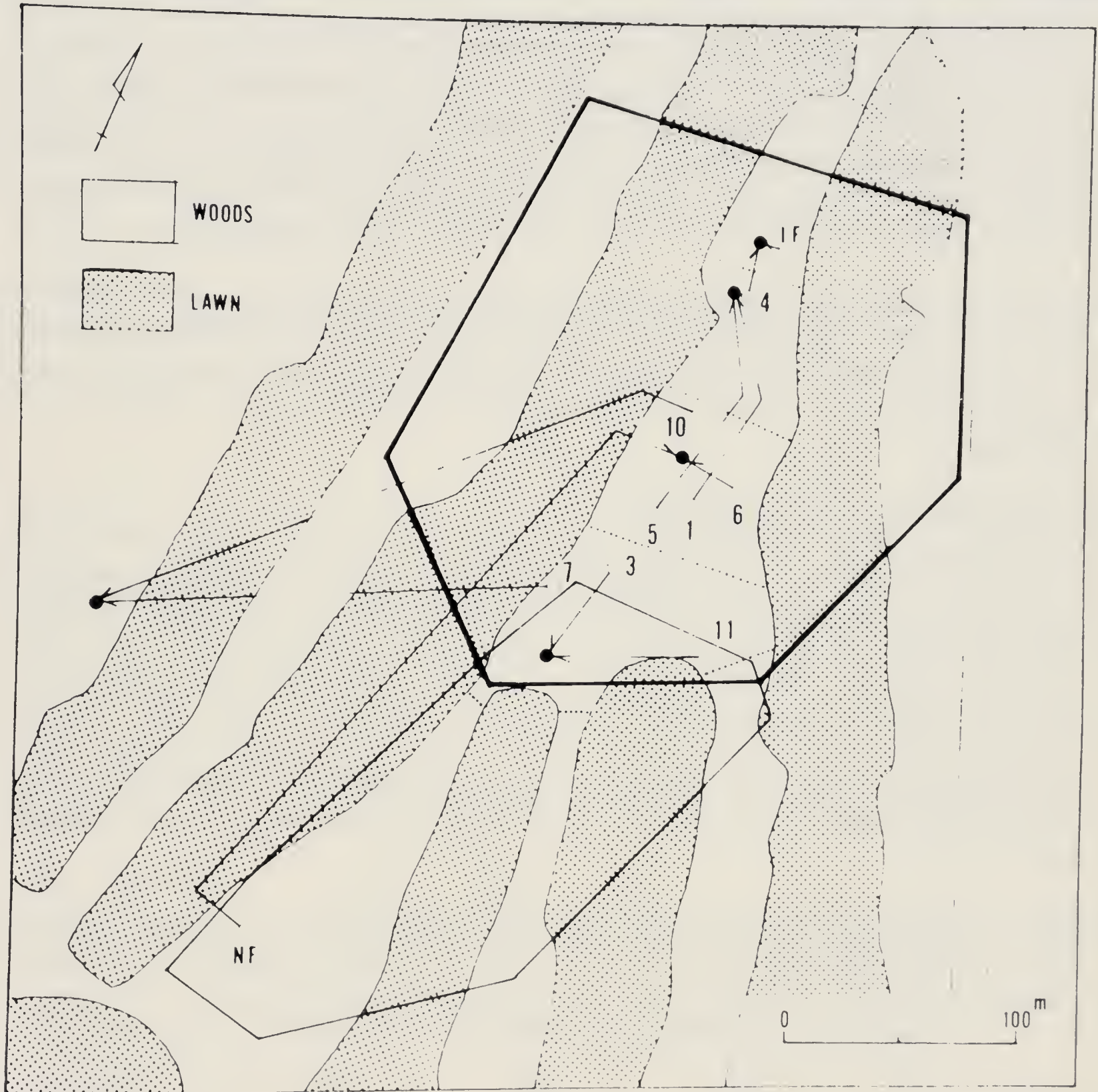


FIGURE 2 - Flock range and territories of flock members. Figures show flock members in Figure 1. Polygon, flock range. Dotted line, boundary of territory in 1987. Black circle, breeding site. Open circle, roosting site. NF, female of neighbouring flock. IF, immigrant female.

RESULTS

Previous histories of breeding pairs

The number of breeding pairs varied between 95 and 115, with an average of 104 ± 8 pairs. Out of a total of 414 pairs studied over four years, there were far more RR pairs (68.1%) than II pairs (11.1%), and RI pairs were intermediate between RR and II pairs. This trend was observed each year, although the number of each pair type varied with year. Since the proportion of RR pairs occupied about two third, it seems

that pair formation took place mainly between residents. In my earlier paper (Saitou 1979c, 1988), I concluded that the flock members usually paired with other members of the same flocks. In this study area, the proportion of pairs between members of the same flock was only 48.1% (199/414 pairs). But each flock differed in the number of males and females. Then I calculated the expected number of pairs from the number of males and females just before the break-up of the flocks; if a flock contains two males and three females, two pairs would be expected. The proportion of the observed to the expected number ranged from 71.2 % to 76.1 %, with an average of 74.5 %. The observed number was similar to the expected number. Therefore, flock members usually paired with other members of the same flock according to the number of males and females in their flocks. The pairs between neighboring flock members were 83 (20.0 %) and 61 pairs bred in the male's flock ranges.

The other 86 residents (59 males and 27 females) paired with immigrants and bred in their flock ranges. The pairs between immigrants consisted of 22 migrants returning to their nests (6 males and 16 females), 14 emigrants from non-overlapping ranges (8 males and 6 females) and 56 immigrants from the surrounding areas (22 males and 34 females).

Age combination of breeding pairs

In the residents (650 birds), there were more OM (34.3 %) and OF (27.1 %) than YM (18.1 %) and YF (20.5 %). This suggests that young birds tend to disperse from their flock ranges. In fact, OM (13.5 %) and OF (22.5 %) were fewer than YM (27.5%) and YF (36.5%) in the immigrants (178 birds). Old immigrants from the surrounding areas were few and most of old birds were migrants (12/24 males and 32/40 females). Out of 414 pairs, there were more OMOF pairs (40.6 %) and YMYF pairs (28.7 %) than OMYF pairs (19.1 %) and YMOF pairs (11.6 %) (Table 1). However, the age combination differed from each other among the three groups. OMOF and YMYF were more than OMYF and YMOF in RR pairs. In RI and II pairs, there were more YMYF than others.

TABLE 1 - Distribution of age combinations of breeding pairs. O, old birds aged two or older. Y, young birds are one year old. M, male. F, female. R, resident. I, immigrant.

Pair	OMOF	OMYF	YMOF	YMYF	Total
RR	144	53	22	63	282
RI	15	19	14	38	86
II	9	7	12	18	46
Total	168	79	48	119	414

Breeding success

Out of 414 pairs, 354 pairs raised at least one young to leave the nest. Table 2 shows that RR pairs laid earlier, had large clutches, fledged more young and produced more surviving young than did II pairs, and RI pairs were intermediate in all four parameters between RR and II pairs. There were significant differences of the mean scores in the laying date between RR and RI pairs ($t = 4.61$, $P < 0.01$), between RR and II pairs ($t = 12.20$, $P < 0.01$) and in the number of young that fledged between RR and II pairs ($t = 2.51$, $P < 0.05$). In the number of young that survived, the difference of the mean score was significant between RR and RI pairs ($t = 2.96$, $P < 0.05$), between RR and

II pairs ($t = 6.08$, $P < 0.01$) and between RI and II pairs ($t = 2.60$, $P < 0.01$). Therefore, RR pairs were more successful than II pairs, and RI pairs were intermediate between RR and II pairs.

The age combinations of pairs were different from each other among the three groups (Table 1). Table 3 shows that RR pairs produced more surviving young in all age combinations than did II pairs, and RI pairs were intermediate between RR and II pairs, again. The differences of the mean scores were significant in YMYF pairs ($t = 3.04$, $P < 0.05$) between RR and RI pairs, in YMOF pairs ($t = 3.25$, $P < 0.01$) and YMYF pairs ($t = 4.02$, $P < 0.01$) between RR and II pairs, but were not significant in other three age combinations between RR and RI pairs or in any age combinations between RI and II pairs.

TABLE 2 - Mean numbers and standardized scores for four measures of breeding success in RR, RI and II pairs. Mean scores in parentheses.

	RR	RI	II	P		
				RR-RI	RR-II	RI-II
No of pairs	243	68	43			
Laying date (April)	19.4 (-0.21)	23.3 (0.40)	24.7 (0.60)	0.01	0.001	n.s.
Clutch-size	8.81 (0.10)	8.65 (-0.01)	8.43 (-0.05)	n.s.	n.s.	n.s.
No. of young fledged	7.59 (0.08)	7.41 (-0.06)	6.88 (-0.26)	n.s.	0.05	n.s.
No. of young survived	1.57 (0.19)	1.21 (-0.13)	0.72 (-0.49)	0.05	0.01	0.05

TABLE 3 - Mean numbers and standardized scores of surviving young in four age combinations of RR, RI and II pairs. Mean scores in parentheses.

	RR	RI	II	P		
				RR-RI	RR-II	RI
OMOF	1.64 (0.14)	1.45 (0.08)	0.80 (-0.48)	n.s.	n.s.	n.s.
OMYF	1.17 (-0.18)	1.00 (-0.15)	0.50 (-0.59)	n.s.	n.s.	n.s.
YMOF	1.70 (0.26)	1.38 (-0.06)	0.88 (-0.59)	n.s.	0.05	n.s.
YMYF	1.70 (0.50)	1.13 (-0.27)	0.68 (-0.50)	0.05	0.05	n.s.

As mentioned above, type A migrants bred in or near their previous breeding areas. In order to know the effect of familiarity with the future breeding area on the number of young that survived, it is better to exclude type A migrants from RI and II pairs containing old birds. The number of those birds was 7 of 12 OMOF, 0 of 15 OMYF and 3 of 14 YMOF in RI pairs, and 5 of 8 OMOF, 1 of 6 OMYF and 6 of 12 YMOF in II pairs. Then I re-examined the number of surviving young of OMOF, OMYF and YMOF in RI and II pairs. The differences of the mean scores were significant in OMOF ($t = 5.39$, $P < 0.01$) and YMOF ($t = 2.49$, $P < 0.05$) between RR and RI pairs. Also, there was a highly significant difference in OMOF ($t = 8.18$, $P < 0.001$) and the probability was higher in YMOF ($t = 9.89$, $P < 0.001$) than that in Table 3 ($P < 0.01$) between RR and II pairs. Since there were none or one type A migrant in OMYF of RI and II pairs, respectively, the results were the same in Table 3. Therefore, RR pairs produced significantly more surviving young in three out of four age combinations than did RI and II pairs.

DISCUSSION

Since the residents are those that breed within their own flock ranges, the degree of familiarity with the future breeding area is high in RR, medium in RI and low in II pairs. Comparing breeding success among RR, RI and II pairs, the familiarity with the future breeding area seems to affect several aspects of breeding success. From the point of view of natural selection, the most important factor is the number of young that survived to maturity. In this respect, there were significant differences among the three groups; RR pairs were more successful than II pairs, and RI pairs were intermediate between RR and II pairs.

The result must be interpreted with caution, however, since the age of individuals has an important effect on several aspects of breeding success (Perrins & McCleery 1985, Perrins & Moss 1974). Perrins & McCleery (1985) reported that OMOF pairs produced more surviving young than did YMYF pairs. As shown in Table 1, the distribution of four combinations of pairs differed from each other among the three groups. There were more OMOF in RR pairs, while YMYF occupied the greatest proportion than others in RI and II pairs. The significant differences in the number of surviving young may be partly due to the differences of age combinations among the three groups.

From the comparison of the number of surviving young between same age combination, RR pairs also produced significantly more surviving young in three out of four age combinations than did RI and II pairs. In RR pairs, both male and female increased their knowledge of the future breeding area throughout the previous winter and could now know where to find food most efficiently in the breeding season; RR pairs are therefore in a better position to provide for their brood. If this were the case, it might explain why the familiarity with the future breeding area had an important effect on the number of young that survived.

The familiarity with the future breeding area is probably more important to young pairs breeding for the first time than to old pairs. In winter, the dominant-subordinate relationship was observed among flock members (Saitou 1979b). Old birds always domi-

nated over young birds within a sex group. The dominant relationship had an effect on the establishment of territories among males (Saitou 1979c). Old birds occupied favorable areas for territory within flock ranges. On the other hand, young birds established their territories in the vacant space of the flock ranges, or were forced to disperse from their own flock ranges to breed in unfamiliar areas. For young flock members, it is important to stay within their own flock ranges; remaining young pairs produce more surviving young than those dispersing from their own flock ranges.

Although the Great Tit is resident in most of the temperate region of Eurasia, breeding success has not been discussed in relation to non-breeding biology. The result reported here support strongly that familiarity with the future breeding area has an important effect on breeding success. Therefore, it is important for the understanding of breeding biology to learn non-breeding biology.

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ARE WINTER DOMINANCE, SPACING AND FORAGING BEHAVIOURS RELATED TO BREEDING SUCCESS IN SILVEREYES?

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ABSTRACT. Individually colour-banded Silvereyes on Heron Island, Great Barrier Reef, were observed in agonistic encounters at feeding stations and in other daily activities in the winters of 1988 and 1989, and dominance, flocking habit, range size and foraging substrate of individuals in winter were examined in relation to breeding success as measured by the number of successful clutches that the birds produced in the subsequent breeding seasons (1988/89 and 1989/90). There were significant year to year and age differences in the results, but successful breeders tended to be less dominant females, solitary or paired foragers, small range holders and *Pisonia* feeders in the previous winter.

Keywords: Silvereye, *Zosterops lateralis*, island population, dominance, flocking, foraging, breeding success.

INTRODUCTION

Many passerine species have two distinct social phases between breeding and non-breeding seasons (Lack 1968); typically they breed in territories in summer and flock in winter. Most studies on social organisation have concentrated on either the breeding season or the non-breeding season, and few followed the same individuals through the two phases over a year or more (e.g. Nolan 1978). The Capricorn Silvereye *Zosterops lateralis chlorocephala* on Heron Island, Great Barrier Reef, is resident but many individuals, particularly younger birds, forage in flocks outside the breeding season (Kikkawa 1980, Catterall 1985). Flocks include sexual pairs whose breeding territories are within the flock's range. Most first-year birds form flocks soon after they become independent and increase their ranges in winter (Catterall et al. 1989). Flocks are loosely organised and their membership often changes. Older birds may forage singly or in pairs near their summer territories and, although they may be found with other birds, especially at some point food sources such as female fig trees (Catterall et al. 1982), they do not stay with flocks.

Dominance behaviour at point food sources results in differential energy intake (Catterall 1989) and affects survival through the winter (Kikkawa 1980). It is also related to breeding success which is considered to reflect, among other factors, the ability of dominant birds to defend territories in areas with the best food supply (Catterall et al. 1982, Kikkawa & Wilson 1983). Other components of the birds' day to day activities in winter may also be determinants of breeding success, and hence of individual fitness. In this paper we test whether certain behaviours in the non-breeding phase are related to the breeding performance of individuals.

METHODS

The Silvereyes of Heron Island have been individually colour-banded since 1964 and the age of each bird is known. For the description of this population see Catterall (1985), Catterall et al. (1982, 1989), Kikkawa (1980, 1987) and Kikkawa & Wilson (1983). Data on individuals were collected in the winters of 1988 and 1989 and were examined in relation to their breeding performances during the 1988/89 and 1989/90 seasons, respectively. It was necessary to separate the two seasons because the population density and breeding success differed markedly between the years (Table 1). We considered only the birds that survived sufficiently long into the breeding season for nesting to have occurred (November). The first-year birds were treated separately from older birds.

TABLE 1 – Population density and breeding success of Capricorn Silvereyes on Heron Island in 1988/89 and 1989/90 seasons.

Winter population			
	Juveniles	Adults	Total
1988	170	355	525
1989	218	253	471
Summer population			
	First-year Birds	Older Birds	Total Young Produced
1988/89	133	294	506
1989/90	139	205	558

Dominance scores were obtained at feeding stations set up in different parts of the island in winter. Altogether 2731 and 2481 encounters involving 360 and 354 individuals were recorded in 1988 and 1989, respectively. As in previous studies (Kikkawa 1980, Kikkawa et al. 1986) only the birds with five or more encounters (247 individuals) were considered and for a preliminary analysis (Table 2) they were classified into dominant (winning more than 2/3 of agonistic encounters), intermediate (between 2/3 and 1/3) and subordinate (less than 1/3) classes. Because the mean dominance score is known to differ between sexes (Kikkawa 1987), the sexes of adults were treated separately.

Observations of daily activities were made over the island in winter while no feeding stations were operated. Each winter several observers patrolled the island systematically each day for two weeks. Individuals encountered during these patrols were identified, and records of their behaviour at the time of first sighting were taken, including location on the island (X and Y coordinates), plant species or substrate of first foraging action observed, and group size. A total of 2716 records was obtained from 442 individuals in 1988 and 2388 records from 382 individuals in 1989. Only the individuals recorded five or more times (403 individuals) were used for analyses. All records for each of these individuals were then used to calculate the following variables: the percentage of records in which the bird was observed singly or in pairs, a range size index (calculated as the square root of the product of the standard deviations of the X and the Y coordinates of all records for the individual), the percentage of records in which the individual foraged in *Pisonia* trees, and the percentage of

TABLE 2 – The number of individuals in different categories for which behavioural and breeding data were obtained.

(a) Dominance				
	Dominant	Intermediate	Subordinate	Total
1988 age <1	8	15	18	41
age >1 M	48	20	5	73
F	23	17	5	45
1989 age <1	15	16	2	33
age >1 M	25	11	2	38
F	8	5	4	17
(b) Group Size (incidences of being paired or alone)				
	<10%	10-40%	>40%	Total
1988 age <1	24	23	5	52
age >1 M	10	32	42	84
* F	8	25	34	67
1989 age <1	22	26	15	63
age >1 M	3	28	46	77
* F	1	21	33	55
(c) Range size index				
	Small (<15)	Intermediate (15-25)	Large (>25)	Total
1988 age <1	16	13	23	52
age >1 M	40	28	16	84
F	25	24	18	67
1989 age <1	21	19	23	63
age >1 M	52	22	3	77
F	34	16	5	55
(d) Foraging incidences in <i>Pisonia</i>				
	<10%	10-40%	>40%	Total
1988 age <1	39	12	1	52
age >1 M	26	42	16	84
F	22	29	16	67
1989 age <1	31	19	13	63
age >1 M	12	31	34	77
F	12	17	26	55

TABLE 2 – cont.

(e) Foraging incidences on scraps					
	<10%	10-30%	>30%	Total	
1988 age <1	18	16	18	52	
age >1 M	46	27	11	84	
F	36	20	11	67	
1989 age <1	53	7	3	63	
age >1 M	67	6	4	77	
F	48	5	2	55	

(f) Breeding success (number of nests that fledged young)					
	0	1	2	>2	Total
1988/89 age =1	35	17	0	0	52
age >1 M	20	36	27	1	84
F	13	29	23	2	67
1989/90 age =1	35	19	9	0	63
age >1 M	12	25	21	19	77
F	5	14	18	18	55

* Differences between sexes: 1988: G = 0.01, df = 2, P > 0.99; 1989: G = 0.001, df = 1, P > 0.95

records with foraging on scraps. Birds could then be placed into one of the frequency classes for a preliminary test of age and sex differences (Table 2). For this test the few individuals of unknown sex among the older birds were excluded.

Since the Silvereyes are multibrooded (Kikkawa & Wilson 1983), breeding success was measured by the number of nests from which at least one young fledged. If no young was fledged it was treated the same as when no nesting attempt was made. Many first-year birds did not breed, but up to five successful broods were raised over six months by older birds. Most birds attempted two or three clutches and fledged two young per successful nest.

RESULTS

Table 2 shows sample sizes of different categories of birds for which winter activity and breeding success data were obtained. Sexes did not differ significantly in group size, range size, foraging in *Pisonia* or on scraps. Thus apart from dominance the sexes were combined for further testing. Also, the birds with two or more successful nests were grouped to increase sample sizes for tests of significance. A highly significant matching of sexes in the frequency of being found singly or in pairs (Table 2b) is probably due to the association of sexual pairs in foraging.

Figure 1 shows the relation of winter dominance to breeding success. Many first-year birds did not breed, especially in the 1988/89 season. However, the first-year males

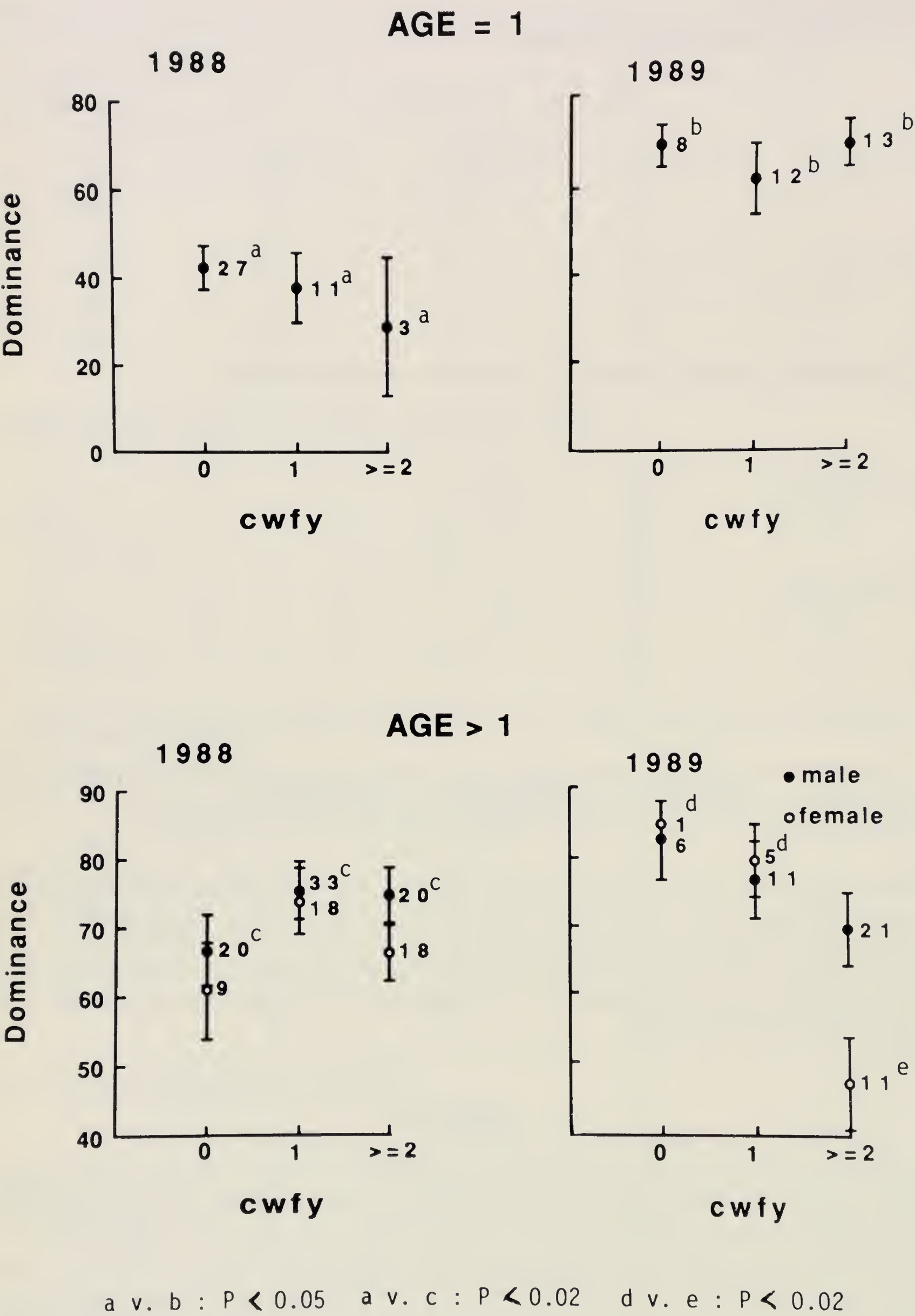


FIGURE 1 – Means (dots) and standard errors (bars) of % wins (dominance) of individual birds (figures indicate sample sizes) observed in five or more agonistic encounters in winter according to the number of successful clutches the birds produced (cwfy) in the subsequent breeding seasons.

that produced fledged young tended to be dominant (Table 3) though this was not significant statistically. Among older birds those that produced two or more successful clutches in 1989/90 were not as dominant as less successful breeders, especially among the females.

TABLE 3 – The numbers of first-year males of known dominance status according to whether they produced fledged young or not.

Fledged Young	Produced	Not produced	Total
dominant	9 (1)*	9	18
intermediate	4(1)	12	16
subordinate	2 (0)	6	8

G = 2.80, df = 2, P> 0.20

* The figure in brackets indicates the number of first year males that produced more than 2 fledged young.

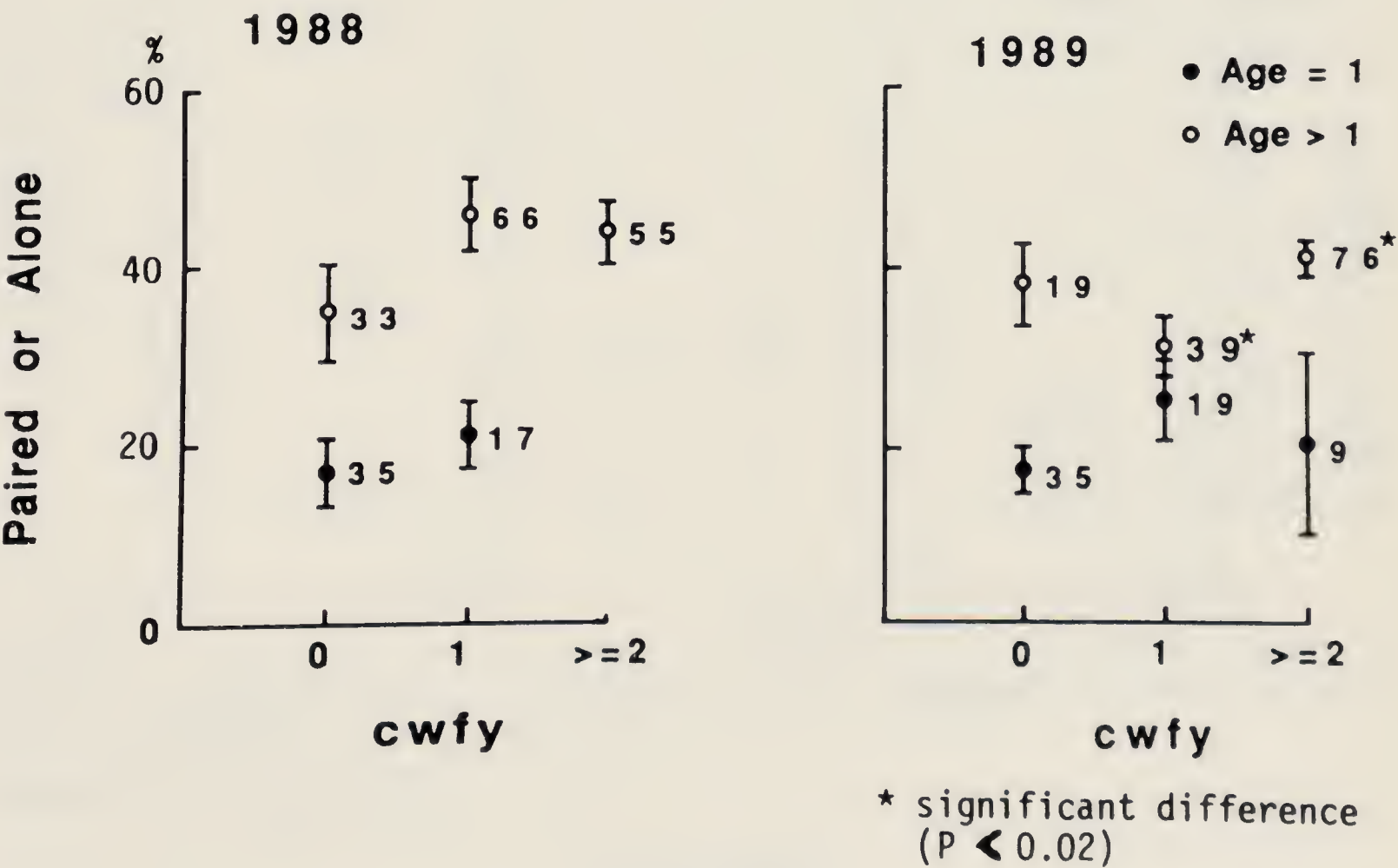


FIGURE 2 – Means and standard errors of % incidences of individuals being observed in a pair or alone during winter foraging according to the number of successful clutches the bird produced in the subsequent breeding season.

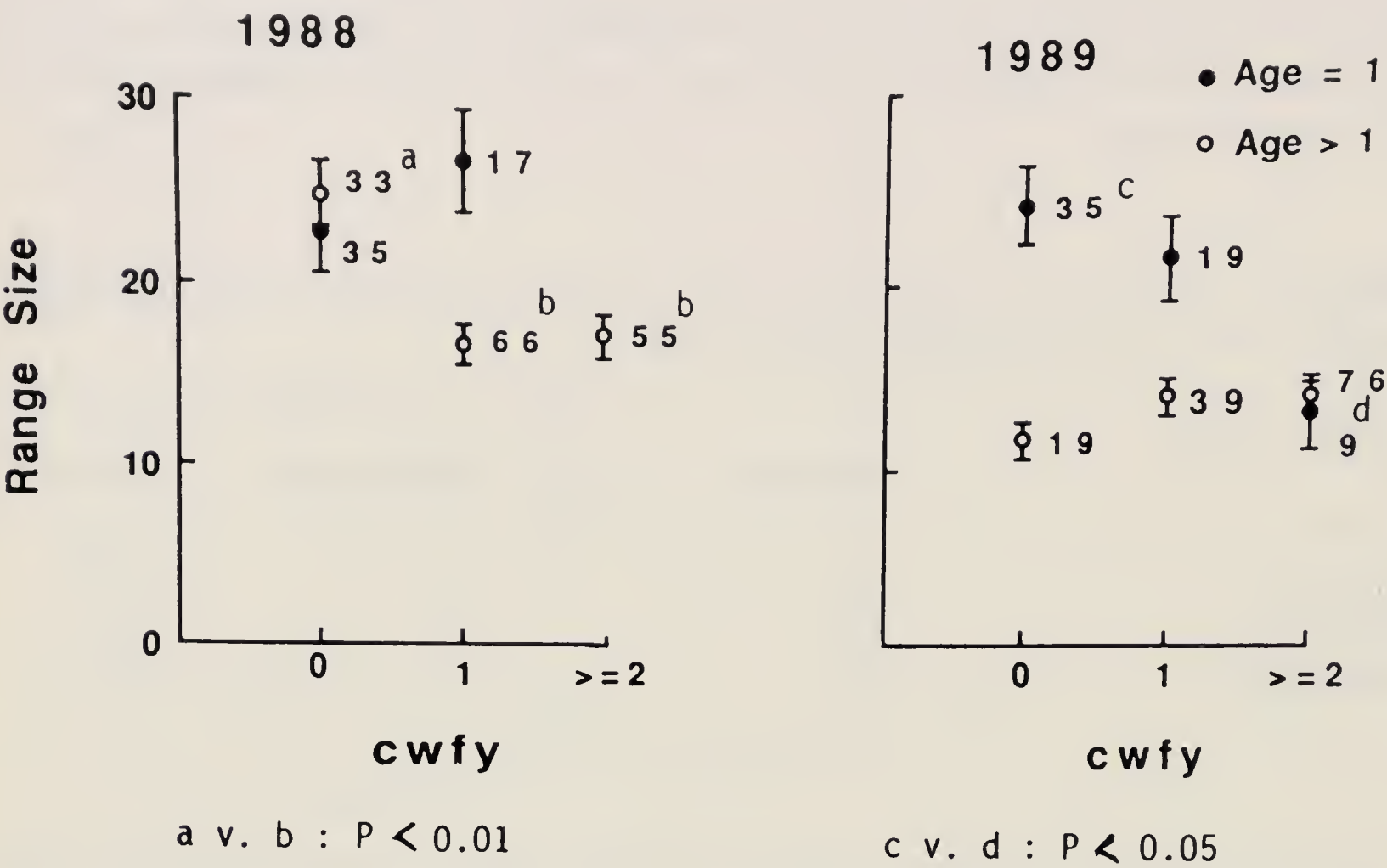


FIGURE 3 – Means and standard errors of range size index (greater the value the larger the range, see text for explanation) of individuals observed in winter foraging according to the number of successful clutches the bird produced in the subsequent breeding season.

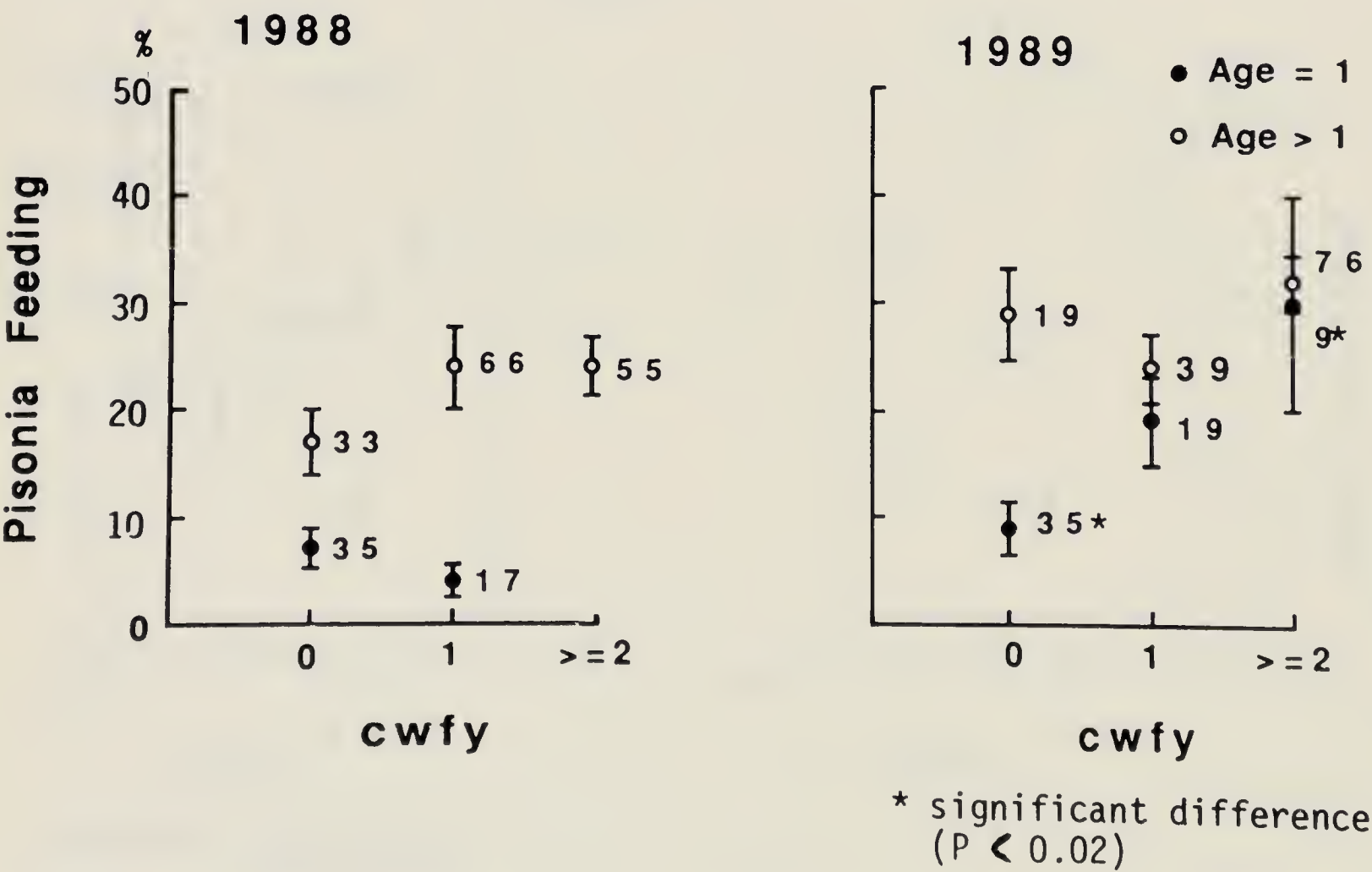


FIGURE 4 – Means and standard errors of % incidences of individuals being observed foraging in *Pisonia* trees in winter according to the number of successful clutches the bird produced in the subsequent breeding season.

Figure 2 depicts the relation between the frequency of non-flocking (solitary or in pairs) in winter activities and breeding success. Except for the first-year birds which were less likely to be found alone or in pairs away from flocks in winter than older birds, the birds not flocking in winter tended to produce more successful clutches than the flockers.

Figure 3 relates winter range size to breeding success. The first-year birds tended to range more widely than older birds, and the birds that had smaller winter ranges tended to produce more successful clutches. However, this last tendency was reversed in the first-year birds in 1988 while it was not shown in older birds in 1989.

Figures 4 and 5 show the relations between the frequencies of winter foraging in *Pisonia* trees and on scraps, respectively, and breeding success. The birds that fed in *Pisonia* trees in preference to other places in winter tended to produce more successful clutches than others and this tendency was significant for the first-year birds in 1989. Scrap feeding in winter tended to be advantageous for some first-year birds but successful nesters among the older birds depended little, if at all, on scraps in winter.

Thus winter behaviour had some significant relationships with breeding success when age groups are considered separately; in particular, dominant first-year males, non-flockers, *Pisonia* foragers and small range holders tended to produce more successful nests than others.

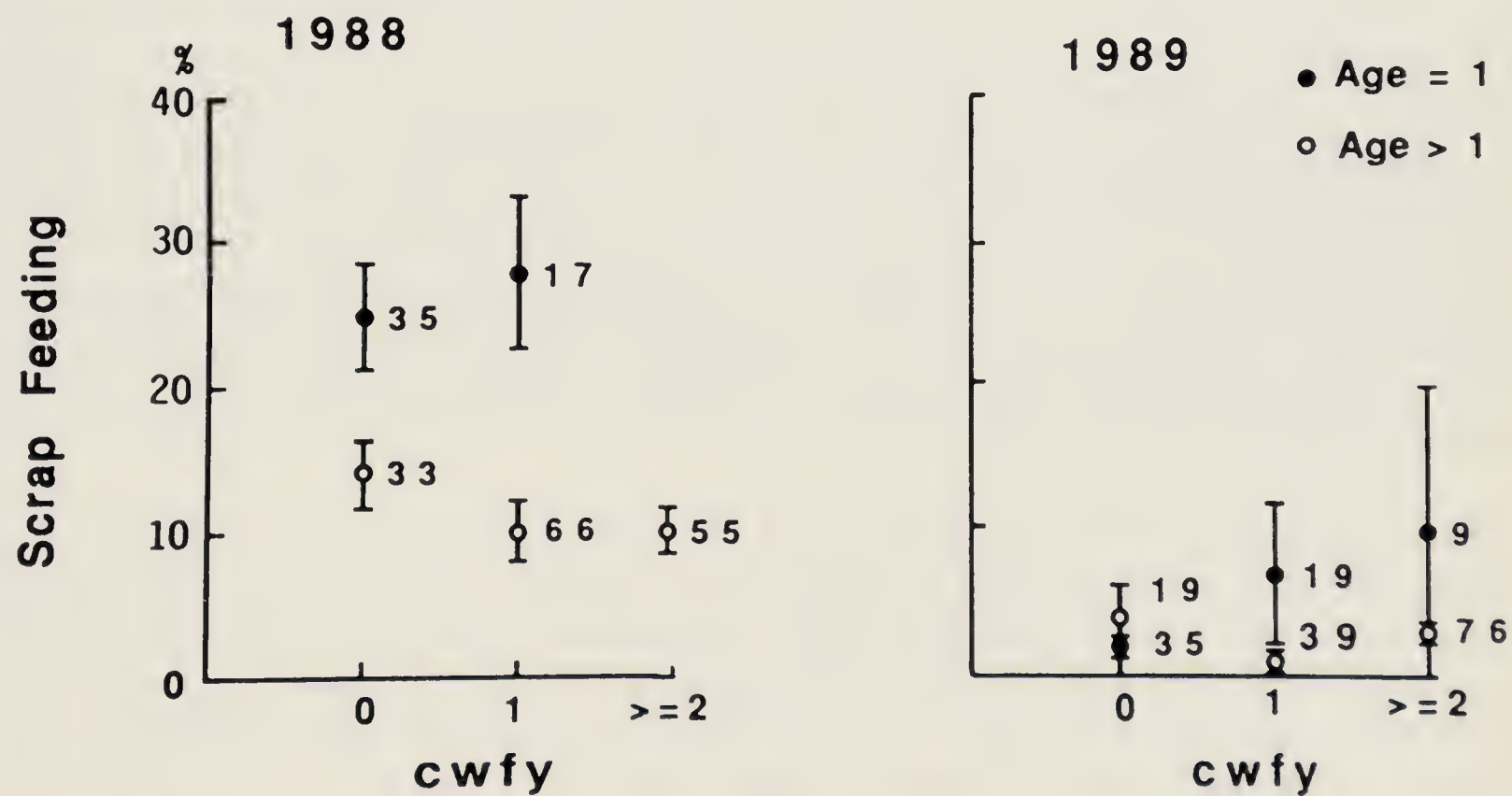


FIGURE 5 – Means and standard errors of % incidences of individuals being observed foraging on scraps in winter according to the number of successful clutches the bird produced in the subsequent breeding season.

DISCUSSION

Fitness of seasonally breeding birds may be divided into two components, survival in winter and reproduction in summer. In the non-breeding phase individuals maximise their chances of survival by escaping predators and finding sufficient food each day, while in the breeding phase these birds try to maximise chances of raising young.

Winter behaviour sampled here is not only indicative of strategies for survival (Kikkawa 1980, Catterall et al. 1982, 1989), but also of individual quality that is considered to influence future breeding success. For example, dominant birds may be able to defend their territories more effectively than subordinate birds (Kikkawa & Wilson 1983, Bruce 1989). Non-flocking birds in winter may be specialised feeders or highly skilled foragers that do not benefit from association with other birds. They may also defend their territories throughout the winter (Catterall 1989, Catterall et al. 1989). In any case, if they can obtain sufficient food within a small range they do not have to range widely in winter. These birds may stay close to their summer territories and may be able to start nesting early and to continue, in fact, to monopolise these areas through the breeding season.

In areas which contain *Pisonia* trees, experienced birds have an advantage over unskilled birds in obtaining good quality food in both winter and summer (Catterall et al. 1989, Jansen 1990). *Pisonia* trees provide most suitable nest sites (Kikkawa & Wilson 1983) and a source of large insects (Catterall et al. 1989), which are important food for young nestlings (Catterall et al. 1982). Scraps were utilised by first-year birds more than by older birds, especially in 1988, at which time the adult density was high in winter and also more scraps were available.

In the present study winter dominance was not related positively to the number of successful clutches produced by the individuals. In fact, the contrary trend became significant among older birds in the 1989/90 season when the birds producing two or more successful clutches were middle ranking females and dominant males which were on average not as dominant as those that produced fewer successful clutches (Figure 1). This result was not expected from the earlier work (Kikkawa & Wilson 1983) in which the dominant class of birds was shown to have produced the greatest proportion of fledged young. One explanation is that because many low ranking birds were not in the sample (except among the first-year birds in 1988) their low breeding success was not represented in the present study. The sample was biased towards a few dominant birds that distributed their pecks to a large number of subordinate birds which were not sampled. This is supported by the trend shown in Table 3.

Another explanation is that, because there are more dominant males than dominant females and thus a pair is likely to consist of a dominant male and a less dominant (or a subordinate) female (Kikkawa 1987), the female's submissiveness may somehow mitigate the disruptive effects of frequent territorial fights on breeding. In this sense it is interesting to note that low breeding success was shared by most dominant males and most dominant females though this occurred in a relatively low density year (Figure 1).

Our results show also that older birds tended not to form flocks in winter but range in small areas around their summer territories where they fed in *Pisonia* trees. Breeding success as measured by the number of successful clutches was highest among those birds that exhibited such trends most strongly. Thus it is important to recognise reproductive success not simply as a product of breeding season activities but as part of an overall life cycle strategy involving behaviour throughout the year.

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MATE REPLACEMENT DURING THE NON-BREEDING MONTHS IN TROPICAL HOUSE WRENS

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ABSTRACT. House Wrens in lowland central Panama are typically dispersed as permanently monogamous pairs on a limited number of territories defended throughout the year. Floater males, females, and pairs exist during both breeding and non-breeding months. Combining both passive replacements of missing residents and active territory takeovers, 36 of 91 mate replacements over a 5-year period, involving a study population of 55 pairs, occurred during non-breeding months. Future mates were accepted in all 24 cases of takeover. Acceptance of a mate is not associated with advantages of age or experience on future reproductive success. Residents did not defend mates during takeover. Mate choice thus appears to be based on the physical condition of contestants. The advantage of "accepting the winner" may be that mate's increased ability to defend the territory from pairs during the remaining non-breeding months, and to resist takeovers during the breeding season that typically lead to infanticide of eggs, nestlings, and even fledglings.

Keywords: House Wrens, *Troglodytes aedon*, monogamy, mate choice, territory takeover, infanticide, non-breeding season.

INTRODUCTION

The annual cycle of most wild birds includes a limited breeding season shaped by temporal variation in food resources, weather, and predator abundance (Murton & Westwood 1977). Within this cycle, the study of mating systems and mate choice has typically focused on events that occur at the beginning of a breeding season (Wittenberger 1979). Effects of earlier events on mate choice have been considered, but these have generally ignored the non-breeding season. Philopatry of breeding sites and experience with the previous mate are considered aspects of mating systems that transcend the non-breeding months (Rowley 1983). However, social organization and behaviour during the non-breeding period may have significant impact on the mate choice options available to individuals and perhaps even on their reproductive success during the next breeding season. Indeed, questions associated with remating in birds across breeding seasons, usually couched in terms of age and experience (Rowley 1983), are incomplete in the absence of a perspective that includes phenomena during the non-breeding season that may constrain previous mates to reunite or prevent them from doing so (Freed 1987a).

Monogamous species that maintain territories throughout the year provide an exceptional opportunity to identify events that occur during the non-breeding season that alter or maintain mating patterns from one breeding season to the next. There are three categories of factors that can result in changes in mating patterns between breeding seasons. First, mortality of a previous breeder will create a vacancy that will enable another individual to pair with the surviving mate on the original territory. Second, a previous breeder can voluntarily leave the territory (individual behaviour). This can occur in the context of either dispersal, as a life history trait, or abandonment of

a previous mate or territory no longer deemed suitable (Greenwood & Harvey 1982). Third, a previous breeder may be evicted from the territory by another individual who then pairs with the remaining mate (social behaviour). Social behaviour as a cause of mate replacement may also include takeover of a territory by a new pair.

There are two factors that may constrain pairs to remain together from one breeding season to the next. Limited and unpredictable vacancies on other territories may force an individual that leaves its mate and territory to become a floater and remain thus perhaps into the breeding season. In addition, pairs may be constrained to remain together just to defend the territory against other pairs. Intruding pairs may be neighbours as a continual threat or floaters as an occasional but unpredictable threat.

Here I document the operation and relative importance of these factors in altering and maintaining the mating patterns of tropical House Wrens *Troglodytes aedon* during the non-breeding months. In lowland central Panama, these birds are typically dispersed as permanently monogamous pairs on territories defended throughout the year (Freed 1987a). A striking feature of the population is the existence of territory takeovers during the breeding season, which typically extends from April to October (Freed 1986). Replacement mates destroy eggs and nestlings, and harass and even kill fledglings (Freed 1986, 1987b). Therefore a potential criterion of mate choice during the non-breeding months may be the condition of a prospective new mate not only to defend the territory during the remainder of the non-breeding season, but also to resist take-overs during the next breeding season.

METHODS

Data concerning mate replacements and behaviour during the non-breeding months were collected from a population of 54-56 pairs of House Wrens studied almost continuously between February 1982 and February 1986. These pairs occurred on stable territories located in a 140 ha study site consisting of partially shaded pastures, shrubby fields, and gallery woodland within a matrix of second-growth forest 25 km northeast of Panama City. Birds were trapped in nest boxes or in mist nets and colour-banded during the breeding season (131 males, 121 females). Pairs were identified during the last nesting attempt of the breeding season (September or October) and thereafter usually 2 or 3 times per month throughout the non-breeding season. Attention was directed at particular pairs or territories for up to 30 minutes. If a particular bird was not seen by this time, it was considered missing. Behavioural observations were made during these inspections and during general presence on the study site.

RESULTS

Mate changes occurred in 42% of the 85 cases over 1982-1985 in which at least one of the two mates at the end of one breeding season was present at the beginning of the next. This is a higher rate of change than the 18% of 306 re-matings that occurred within breeding seasons (chi-square test, $P < 0.0001$). In addition, there were 14 cases during the non-breeding season in which both previous mates disappeared.

Only one case of re-mating between breeding seasons was based on individual behaviour that involved abandonment of a territory and mate (Table 1). This exceptional case occurred when a female mated with a bigamous male for the final clutch of the season left that male and was paired with a neighbouring male whose mate had recently disappeared. Three additional cases in which both mates were still alive and paired with other individuals were caused by eviction of one of the mates during a takeover. The residential bird paired with the takeover individual while the evicted mate became paired later with a bird on another territory.

TABLE 1 - Factors contributing to changes in mating patterns between breeding seasons.

Cause of change	# Cases
Mortality	16
Individual behavior	
Dispersal	0
Abandonment	1
Social behavior	
Takeover by individual	30
Takeover by pair	6

There was no evidence of breeding dispersal on the part of either males or females. Both males and females banded as nestlings dispersed from their natal territory (natal dispersal) before becoming established with a mate on a territory. Some of these birds survived through several annual cycles and remained on the same territory throughout each year. Other long-lived individuals of each sex, of unknown age, generally remained on the same territory throughout their adult life and without regard to previous reproductive success (Freed 1986,1987a).

Mortality accounts for at least 30% of the changes in mating patterns between seasons (Table 1; see below). Mortality was inferred when a colour-banded mate was missing during two consecutive surveys and the other mate was seen alone. There were no instances in which a bird missing this long was seen elsewhere in the study area. Such a pattern of replacement was noted in 16 out of 93 cases (11 times during the 85 cases in which at least one mate was present at the start of the next breeding season, and five times during the eight cases in which neither mate survived but were missing at different times during the non-breeding season).

Social behaviour accounts for up to 68% of changes. These were inferred as territory takeovers when a previously observed resident was already replaced by an individual of the same sex when first detected to be missing. Direct observation of a territory takeover, two fights between non-neighbouring males, and three fights between non-neighbouring females during the non-breeding season indicate that many of these replacements were caused by eviction. At least three individuals who were suddenly replaced were seen elsewhere on the study site, indicating that mortality could not have been involved. Also, many residents who had lost a mate to mortality did not receive a replacement by the next survey (1.5 - 2 weeks later), indicating that mortality and quick replacement were unlikely to account for many of the cases of inferred takeover by individuals. I thus assume that most replacements of a recently observed resident are caused by takeovers. While this assumption may overestimate the actual

number of takeovers, the number of cases of known and suspected takeovers greatly exceeds the number of cases of mortality.

TABLE 2 - Responses of mates to different types of intruder during the non-breeding season

Intruder	Defender		
	Male only	Female only	Pair
Male only	3	0	1
Female only	1	3	1
Pair	0	0	4

Social behaviour also accounts for the six cases in which both mates were replaced simultaneously between breeding seasons. Takeover of one residential pair by a non-neighbouring pair was witnessed in one case. In addition, three fights without replacement were observed between non-neighbouring pairs (2) and neighbouring pairs (1). Given the rapidity of replacement of both mates, I assume that most if not all of the cases of simultaneous pair replacement are the result of takeovers by pairs. In addition, there was a case in which an unpaired bird was displaced by a pair.

Takeovers by single intruders, which are the most prevalent sort (Table 1), provide the mate of the opposite sex with an opportunity to defend their current mate against the intruder or to accept the winner of the takeover attempt as the mate for the next breeding season. Thirteen fights were observed during the non-breeding months in which the sex and number of intruders and defenders were ascertained. In these fights both members of the residential pair were present, so the absence of defence can be inferred by failure of an individual to defend its mate. As shown in Table 2, there is strong and significant agreement in gender and number between intruders and defenders ($K = 0.66$, 95% confidence interval = 0.34, 0.98; Bishop et al. 1975). In the four cases in which pairs contested, the interactions were sex specific. The agreement between sex and number of contestants corresponds with that observed in fights during the breeding season (Freed 1987a).

DISCUSSION

In tropical House Wrens, changes in the composition of the mating population occur throughout the year but are of greater magnitude during the the non-breeding months. Changes at this time are involuntary, involving the death or more frequently the eviction of one or both previous residents. Social behaviour in the form of territory takeovers by individuals and pairs is the major cause of change, and mates generally do not defend one another from intruders. This dynamic has several implications for the form of social organization and for the short-term and long-term benefits of mate choice that occur months before breeding begins.

Territoriality by pairs even during the non-breeding months in these non-migratory birds may be maintained by the presence of pairs in the floater population as well as by aggressive neighbours. As evidenced once during the non-breeding months, and several times during the breeding season (Freed 1987a), single birds tend to be displaced by pairs. Territoriality may thus be an evolutionarily stable strategy (Maynard Smith 1982), able to invade a population of non-territorial pairs or of territorial individuals because territorial pairs would have a disproportionate share of apparently limited breeding territories when breeding commences. Also, a population of territorial pairs would not be invaded successfully by non-territorial pairs or territorial individuals. The former would be unlikely to obtain and the latter would be unlikely to defend territories against territorial pairs.

Within the context of territoriality by pairs as an evolutionarily stable strategy, challenges by single intruders represent an opportunity for the resident of the opposite sex to compare the quality of their current mate and the intruder as future defenders of the territory. If the current mate repels the intruder, that mate has demonstrated a better ability to defend the territory against pairs. If the intruder evicts the current mate, that intruder has demonstrated a better ability for such defence. Therefore, an "accept the winner" strategy of mate choice, for either sex, may increase the likelihood of that individual retaining the territory for the pending breeding season.

That strategy of mate choice during the non-breeding season may have longer-term ramifications that influence reproductive success. Takeovers of individual mates occur during the breeding season and almost invariably result in infanticide of eggs and nestlings (Freed 1986, 1987b). A mate in good condition may be more likely to resist a takeover attempt and prevent infanticide. Given that pairs are constrained to remain together during the non-breeding months, because few vacancies exist on other territories (a total of 16 openings in three years), accepting the winner at that time may be the best option for pairing with an individual that is likely to resist takeovers when there are vulnerable nests.

An "accept the winner" strategy of mate choice during the non-breeding months may result in an inexperienced pair during the breeding season. However, there is substantial evidence in these birds that age and experience have trivial effects on reproductive success (Freed 1987a). Because of this, the most relevant feature of a prospective new mate during the non-breeding months is its ability to defend the territory against pairs at all times and against individuals of the same sex during the breeding season.

The effects of social organization and behaviour during the non-breeding months on mating structure, as observed in tropical House Wrens, may pertain to numerous additional species of birds. Many tropical birds are typically found as pairs throughout the year (review in Kunkel 1974), so floaters are likely to be a continual threat or source of replacement to residents between breeding seasons (e.g. Smith 1978). Detailed study of other species, however, are required to establish the generality of these effects, as well as a fuller understanding of the selective basis for the social organization itself.

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THE FUNCTION OF AUTUMN SONG IN THE SIBERIAN MEADOW BUNTING *EMBERIZA CIOIDES*

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ABSTRACT. Although many studies have considered the function of bird vocalisation in relation to the spring territory, little attention has been paid to the role of the autumn song. In the Siberian Meadow Bunting *Emberiza cioides*, the autumn song seems to serve as an advertisement of settlement or site tenacity, and not as a mechanism of spatial exclusion of conspecific intruders as in the spring territory, despite the similar vocalisation pattern. A high correlation exists between autumn song and the establishment of breeding territory, and 77% of males singing in autumn possessed that singing area the following breeding season. However, the area occupied was not fixed spatially, and was affected by social interactions between residents and newcomers. The ownership of the song area in the autumn suggests a bottle-neck effect in the non-breeding season which regulates the breeding population of the following breeding season.

Keywords: *Emberiza cioides*, autumn song, song area, autumn territoriality, settlement, site tenacity, pre-emptive establishment of breeding territory, population regulation

INTRODUCTION

Although it has long been known that some species of birds sing in autumn (e.g. Howard 1920), the function of the autumn song has not been fully elucidated either ecologically or behaviourally. Many authors have simply considered the autumn song as a partial recurrence of the physiological state of early spring (e.g. Lack 1943).

However, attention has recently been drawn to the possibility that the number of breeders is regulated by territoriality during the previous autumn (Dhondt 1971, Kluyver 1971, Knapton & Krebs 1974). Several workers have tried to clarify the relationships between autumn singing and the rate of settlement in the following breeding season (Falls 1969, Haukioja 1971), but little evidence for an autumn territorial system has emerged and most studies have merely suggested or afforded indirect proof of the importance of this phenomenon.

This study is based on observations of marked individuals of the Siberian Meadow Bunting *Emberiza cioides* in central Japan. In this paper, I first describe the frequency of each individual's autumn song, their sedentariness after autumn settlement and the strong relationship between the areas in which autumn song was sung and the area occupied in the following breeding season. Secondly, I try to show that the ownership of the song area during the autumn, six months prior to the spring breeding, has a bottle-neck effect in the non-breeding season which regulates the breeding population of the following season. Lastly, I will discuss the ecological function and significance of the autumn song in sedentary species.

* Common and scientific names follow Ornithological Society of Japan (1974).

STUDY AREA AND METHODS

The study was made in a flooded meadow grassland (500 x 300 m) situated on the west bank of the Chikuma River (138°7'E, 36°31'N), from 1971 to 1975. This area (the intensive study area) included a running water area of about 2.5 ha. This flooded bed was mainly covered with Gramineae grasses (dominated by *Festuca elatior*) and contained many small pools. Purple willow clumps *Salix gracilistyla* and emergent vegetation (mainly *Phragmites communis* and *P. japonica*) were prominent along the edge of the river and around the pools.

Following capture in mist nets, birds were individually marked by coloured leg bands. Following the post-juvenile moult it was not possible to discriminate juveniles and adults by their plumage, but differences in wing length, facial patterns and iris colour were valid criteria for discrimination until November (Yamagishi 1974).

Marked individuals were continuously observed for one hour, and the positions of each individual at 2.5 min intervals were plotted on map cards (1/2000). Observations were made for 42 days, from September to November, 1972 and 1973. The singing frequency on each day was represented as the percentage (singing loci) of all the activity loci recorded for the individual that day. The total singing frequency of an individual was calculated as a sum of all daily singing frequencies of that individual throughout the autumn song period. The area within which an individual sang, hereinafter termed 'song area', was determined by plotting the outermost singing activity loci to form a polygon. The size of each area was obtained by superimposing each on the map and measuring with a planimeter.

An area of about 44 ha, including the intensive study area, was censused twice monthly 47 times, from May 1970 to April 1972. Censuses generally lasted three to four hours and were completed before noon. The number of birds encountered and the number and position of singing or fighting males were recorded. In addition to these census data, an area of 16 km² was censused for 27 days in 1975 to locate birds which had dispersed outside the intensive study area.

RESULTS

Residents and newcomers

In autumn (October and November), the males in the intensive study area were classified into two residence classes. Males which had lived in the area since the previous breeding season were called 'residents', while those which came into the area after the breeding season were called 'newcomers'. In this paper, females are not discussed.

Residents remained within practically the same territories after the breeding season (Yamagishi 1978). Only five (19.2%) out of 26 breeding males moved into adjacent territories vacated by the original owners. Twenty-four newcomers, consisting of adults (nine) and juveniles (15) were banded (Table 1). Out of 24, five (21%) settled in the study area, five settled outside the study area within 16 km², and 14 disappeared from the area of 16 km² (Table 1). However, many unbanded males were also present in the study area, and the actual rate of settlement in the study area would be less than 21%.

Autumn song

Song could be heard during the periods February-March, May-August and October-November (Yamagishi 1978). The songs sung in autumn are here called 'autumn song' (Figure 1). In the autumn song, the same notes were used as in the breeding season song but their duration was shorter.

TABLE 1 – Differences between residents and newcomers in singing in autumn and settlement in the following spring (in parentheses; A=adult, J=juvenile, ?=age unknown). Type of settlement: I. Settled in the study area, II. Settled out of the study area, IIIa. Temporary stay within study area until end of winter, IIIb. Temporary stay out of study area until end of winter, IIIc. Disappearance after first capture.

	1972			1973			1974		
	Individ- ual	Autumn song	Type of settle- ment	Individ- ual	Autumn song	Type of settle- ment	Individ- ual	Autumn song	Type of settle- ment
Resident	M11 (A)	+	I	M 11 (A)	+	I	M 11 (A)	+	I
	M17 (A)	+	I	M 17 (A)	+	I	M 17 (A)	+	I
	M25 (A)	+	I	M 25 (A)	+	I	M 25 (A)	+	I
	M76 (A)	+	II	M152 (A)	+	I	M152 (A)	+	IIIa
							M395 (A)	+	I
							M396 (A)	+	I
Newcomer	M152 (A)	+	I	M 48 (A)	+	I	M999 (J)	+	I
	•			M343 (A)	+	I	M730 (A)	–	IIIc
	•			M395 (J)	+	I	M910 (A)	–	IIIc
	•			M396 (J)	+	II	M711 (J)	–	II
	•			M a (?)	+	?	M716 (J)	–	IIIb
				M b (?)	+	?	M720 (J)	–	II
				M295 (A)	–	IIIc	M750 (J)	–	IIIb
				M352 (A)	–	IIIa	M911 (J)	–	II
				M368 (A)	–	IIIc	M912 (J)	–	IIIb
				M377 (A)	–	IIIc	M923 (J)	–	IIIc
				M290 (J)	–	IIIc	•		
				M291 (J)	–	IIIa	•		
				M292 (J)	–	II	•		
				M307 (J)	–	IIIa	•		
				M358 (J)	–	IIIc	•		
				•					
				•					
				•					

SINGING INDIVIDUALS. All 14 residents sang in three autumn seasons (1972-1974), whereas among the 24 banded newcomers, only three adults (33%) and three juveniles (20%) sang. Adult newcomers tended to sing frequently, but the factors influencing their singing activities could not be determined. There were no significant differences in the body weight between seven singing residents/newcomers and eight silent newcomers ($P>0.05$, $t=0.2828$). Seventeen adults (73.9%) in the study area sang an autumn song (Table 1).

SINGING PERIOD AND FREQUENCY. Individual singing frequency in autumn (1972 and 1973) is shown in Figure 1. The autumn song began at the end of September and lasted

until the end of November, with a peak from the middle of October to the beginning of November. Residents started to sing earlier in the season than did newcomers. The more singing newcomers present, the more frequently residents sang. In 1972, when only one newcomer (M152) sang, each resident (M11, M17, M25, M76) had a very low total singing frequency (av. 0.76). Conversely, in 1973, when six newcomers (M48, M343, M395, M396, Ma, Mb) sang, residents (M11, M17, M25, M152) sang much more intensively (av. 2.53).

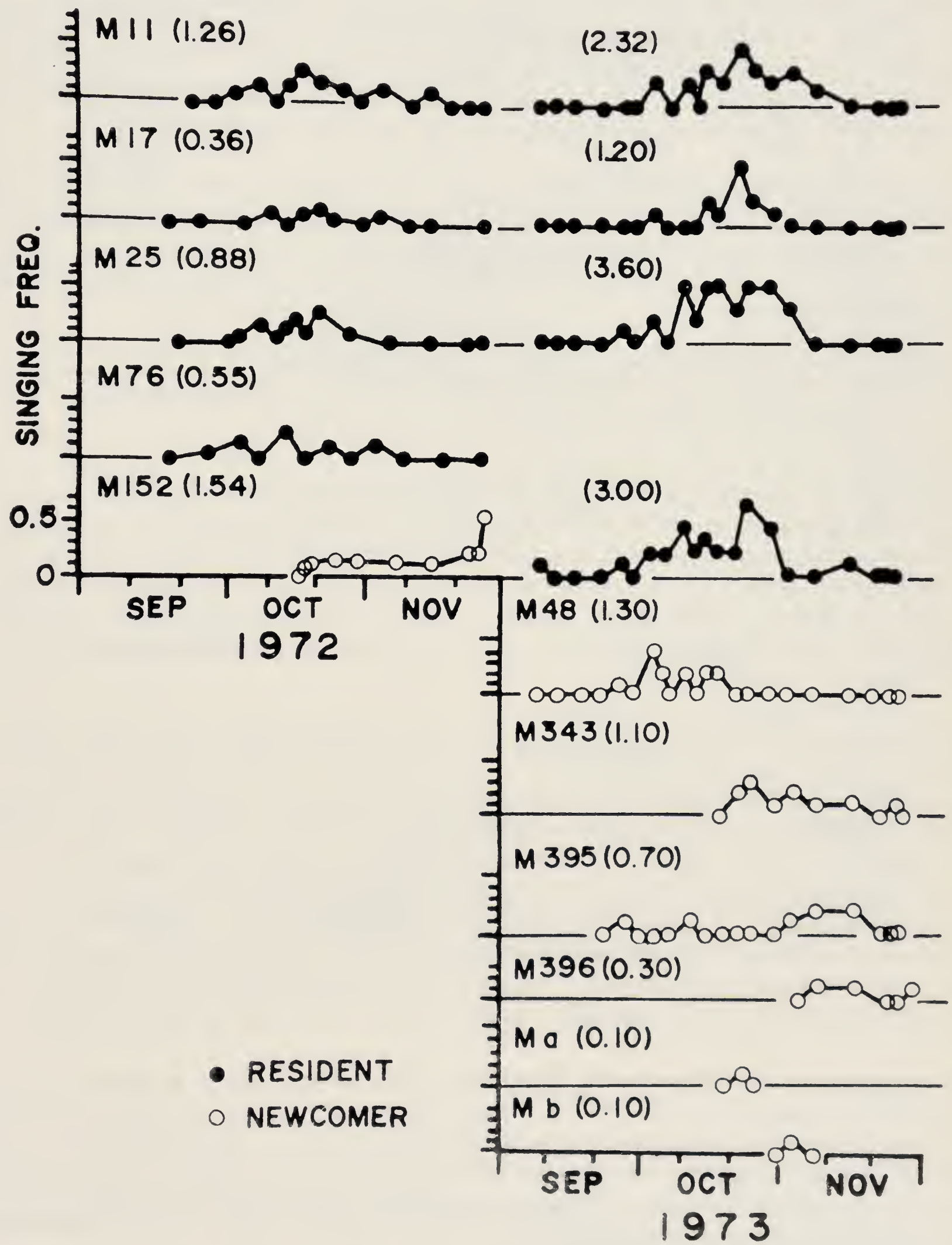


FIGURE 1 – Singing frequency in autumn. Numerals in parentheses are total singing frequencies. See text for details.

There was no clear correlation between autumn singing frequency and possession of a mate. Singing frequency in autumn was generally lower than in spring, and was influenced by adjacent males' singing activities. Since a considerable number of pairs were formed in autumn, the function of autumn song in mate attraction cannot be dismissed.

CORRELATION BETWEEN AUTUMN SONG AND SETTLEMENT IN THE SUBSEQUENT BREEDING TERRITORY. Seventeen birds stayed within the intensive study area until the next breeding season. Of these, all sang autumn song (Table 1). However, among 14 resident singers, two (M76, M152) disappeared from the area. In February 1973, M76 settled 200 m from the study area, where he sang autumn song in 1972. M152 disappeared in December 1974 and could not be located in the 16 km² total survey area.

In comparison, among eight singing newcomers, three (M396, Ma, Mb in 1973) did not continue to stay in the study area. M396 settled 100 m from the study area where he sang autumn song, and moved into the study area again the next autumn as an autumn singer. Ma and Mb were unbanded and no further information was available about their settlement.

Consequently, 77% (17/22) of the males singing in autumn remained within nearly the same area where they sang autumn song until the following breeding season.

Song area

COMPARISON OF AUTUMN AND BREEDING SONG AREAS. A comparison of the distribution of song posts and song areas in autumn (1973) with those in the previous and subsequent breeding song areas is shown in Figure 2. Singing males had a mean of 9.6 song posts in autumn, approximately 33% of the number utilised during the breeding season. In autumn, singing males showed a clear tendency to shift their song posts frequently (0.6 song posts/male/h in the breeding season; 4.1 song posts/male/h in autumn).

The average size of the breeding song area of four residents (M11, M17, M25, M152) was 14,600 m² (12,800-16,800 m², SD = 1428 m²) and 11,700 m² (6400-17,600 m², SD = 3973 m²) in 1973 and 1974, respectively. During autumn, however, the average size of the song area of the same residents was 6000 m² (4000-9200 m², SD = 1980 m²). Although, autumn song areas were considerably smaller than those of the previous and subsequent breeding seasons, they overlapped with these greatly; more so with the song areas of the previous breeding season (av. 30%, 20-55%) than with those of the following breeding season (av. 21%, 8-34%). These findings suggest that the shifts of song areas observed during the non-breeding season are mainly influenced by social interactions between residents and newcomers during the autumn.

ESTABLISHMENT OF AUTUMN SONG AREA. On 49 occasions the behaviour of resident males immediately prior to singing was observed. Seventeen (34.7%) of these were responses to the singing or approach of another resident male. In these cases, the song posts of adjacent resident males tended to be situated close together (Figure 2: top), suggesting that the presence of adjacent resident males plays an important role in establishing the autumn song area.

The presence of newcomers also influenced the establishment of the autumn song area. In 26 (53%) of the above-mentioned 49 instances, resident males started to sing

just after approaching or chasing newcomers. The residents' song posts were located near the positions where newcomers were detected (Figure 2). This tendency was particularly evident in the cases of M17 and M25.

Among the six singing newcomers, the three which settled started to sing earlier than those which did not settle, and remained within nearly the same area until the next breeding season. Two of these individuals, M343 and M395, established their song

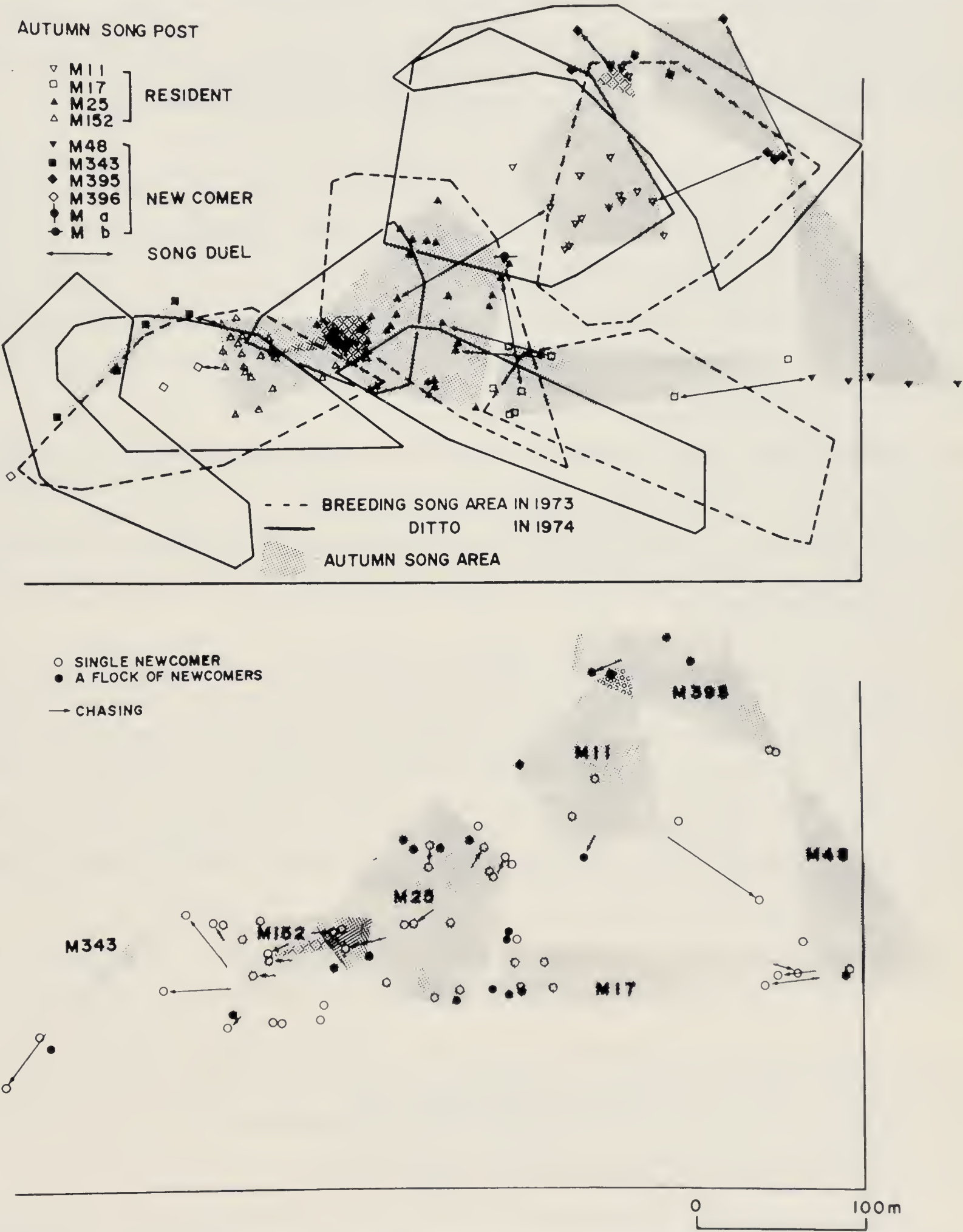


FIGURE 2 – Top: Autumn song posts in 1973 and song areas compared with two breeding song areas in 1973 and 1974. Bottom: Positions at which newcomers were detected by observer. Arrows indicate direction chased.

areas on the gravel bed of the river or at the marginal parts of the flooded bed. As the main winter food of this species is the seed of Gramineae grasses, the habitats occupied may be considered to be suboptimal.

Individual Mb sang at only one song post, whereas M396 had three song posts arranged in a straight line. Ma established a small song area, completely overlapping with the residents' song areas. These three autumn singing newcomers disappeared from the study area.

Results suggest the importance of maintaining a minimum autumn song area (av. 6000 m², SD = 1980 m²) in a preferred habitat to be settled for breeding.

EXCLUSIVENESS OF AUTUMN SONG AREA. The positions at which individuals were detected and the direction in which they were chased are shown in Figure 2 (bottom). An analysis of the 22 chasings recorded in autumn 1973 revealed most (16) to be by resident males to newcomers. Four of the five chasings by newcomers were directed at other newcomers, and only one at a resident male. Only one instance of a resident male chasing another resident was recorded. On two occasions a newcomer who mingled with a flock (2-7 individuals) was chased by residents. In both cases, the whole flock was not driven away, but only the one individual was chased off.

Among chases by residents nine were directed at individuals inside the resident's song area, six times at individuals within a 30 m zone outside the song area, and only once outside this zone 70 m away from the song area. Thus, in autumn also, resident males chased intruding individuals from their song area, restricting them to its periphery or to their own song areas. As in the spring, the song area and territory also seem to coincide in the autumn.

In contrast, male residents were often tolerant of newcomers of both sexes within their autumn song areas (85% out of 35 cases observed). It was unclear just which behaviours of non-singing newcomers evoked an aggressive response by the resident, but when newcomers sang within a resident's song area, they were immediately chased off. Interestingly, despite their similar structure autumn songs alone failed to deter newcomers from entering a resident's song area. This is in contrast to the clear territorial demonstration and repelling effect of the song in the breeding season (Yamagishi 1971).

DISCUSSION

Several authors have postulated that autumn territoriality plays an important role in regulating the breeding population of birds (e.g. Falls 1969, Dhondt 1971, Haukioja 1971, Kluyver 1971). However, the autumn territorial behaviour per se which acts to expel subordinate individuals has not been considered.

The present study shows clearly that autumn song is an advertisement of the territory by residents and by newcomers. It was shown that the ownership of an adequate autumn song area is a prerequisite for the establishment of a breeding territory the following breeding season.

The number of breeders and the positions of breeding territories in the flooded meadow grassland were surprisingly stable over a seven-year study period (Yamagishi 1978). The average rate of adult disappearance throughout the breeding season was 22.5% for males and 50.9% for females. For the whole population, about 2.1 fledglings were reared per pair per season, assuming the disappearance rate of adult females to be constant throughout the breeding season (Yamagishi 1978).

The total number of yearlings which entered the flooded bed in autumn was unknown, but each year seven to eight males and 14-15 females were banded in the intensive study area. These counts were about twice those of fledglings in the study area, indicating a large number of juveniles to be concentrated in the flooded bed until autumn. This recruitment pool of juveniles apparently outnumbered the adult disappearances.

Of the newcomers who sang autumn songs, very few could establish a breeding song area the following season, within or near their autumn song areas. Resident males stayed in the same general area throughout the year (Yamagishi 1978). Especially in autumn, the settlement of male newcomers within or around residents' territories was prevented mainly via territorial exclusion by resident males. Since the flooded bed, a favourable habitat, was compactly covered with a mosaic of resident males' territories, male newcomers could only settle in the spaces vacated by disappeared male residents, or in the spaces between resident territories, or in the peripheral part of the optimal habitat.

In the case of sedentary birds, including Meadow Buntings, it is mainly during the autumn that non-territorial newcomers attempt to settle in the favourable habitat almost completely occupied by territorial males. However, resident males show an extremely strong effect of prior residence, and do not allow subdivision of occupied area into smaller units. The territories of residents thus remain relatively constant and therefore newcomers are able to settle only in empty spaces. In this species, the annual disappearance rate of adult males is relatively small (21.3%) (Yamagishi 1978), so there are few vacant spaces available each year.

From the results of their removal experiment, Knapton & Krebs (1974) proposed that species with a high average adult mortality will show greater annual rearrangements of territory than species with a low adult mortality, where only a single space is created at a time. The case described in the present paper may be that of a species of low adult mortality. Thus, autumn has a bottle-neck effect in the non-breeding season in influencing the lifetime fitness of an individual. Such a system is probably common among sedentary passerine birds.

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NON-BREEDING SEASON ATTRIBUTES OF MALE DARK-EYED JUNCO THAT ACQUIRED BREEDING TERRITORIES IN THEIR FIRST YEAR

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ABSTRACT. In a mountain-breeding population of Dark-eyed Juncos *Junco hyemalis*, most young leave the mountaintop in winter. When males return in their first spring, some get breeding territories whereas others become floaters. In one spring we were able to compare territorial and non-territorial yearlings with respect to age, location(s) occupied in the preceding summer, arrival time in spring, and morphology. The two groups differed only in locations occupied. In a second spring we could analyze characteristics only of territorial yearling males. These had tended to exhibit site attachment in the preceding summer, and the majority had been encountered on the study area in the preceding October; among the latter, most held territories next spring at an autumn site. Our findings suggest that male site attachment forms before or during autumn and that familiarity or a prior residence effect confers an advantage in territorial competition the following spring.

Keywords: *Junco*, yearling males, territorial males, floater males, nonbreeding-season attributes, site familiarity, site attachment, prior residence.

INTRODUCTION

We studied a population of colour-banded Dark-eyed Juncos *Junco hyemalis* in which some males did and others did not acquire territories in their first potential breeding season. Our objective was to find nonbreeding-season attributes that correlate with success in gaining a territory as a yearling.

These juncos breed at high elevations and in winter many, especially young males and females of all ages, move downslope, usually no more than a few km. Except during the breeding season (and, in adults, sometimes during autumn), juncos gather in loose flocks of as many as about 25 individuals. They are apparently monogamous, and males hold large all-purpose territories (Wolf et al. 1990). The sex ratio is male-biased during the breeding season. At least 99% ($n > 125$) of surviving males older than one year reoccupy their last year's territories. Accordingly, we deal here only with yearlings, because only they face a considerable probability of failing to get a territory. We are able to look for associations between nonbreeding-season characteristics and territoriality because natal and juvenile dispersal is quite low. Thus, as a result of our effort to band young in summer, most yearlings that we encounter the following spring are already banded.

* Common and scientific names follow American Ornithologists' Union (1983).

We present two classes of data. First, we summarize population-level information (unpublished unless accompanied by a citation). Second, we analyze data from males that were and males that were not banded as young, that survived the winter, and that were present next spring as yearlings. We divide these into individuals that gained territories on our study area at the beginning of the breeding season and those that did not (hereafter, territorial and non-territorial males, regardless of the season we are speaking of). Some non-territorial males undoubtedly leave the study area in spring and breed elsewhere, which weakens the attempt to detect differences between them and territory holders and makes our comparisons conservative. Nevertheless, we believe that juncos that were present on the area as young and that, in most cases, left it in winter and returned next spring may be regarded as probably having sought a territory there. We recognize that failure to gain a territory may not be the equivalent of failure to father young.

We predicted, as possible advantages possessed by territory-seeking males, traits or behaviour in the first summer, autumn, and winter of life that might confer dominance (Arcese & Smith 1985), perhaps as the result of site familiarity (Yasukawa 1979) or a prior residence effect (Cristol et al. 1990). Therefore for two years we analysed date of hatching, date of first capture after attainment of independence, frequency of captures and sightings (hereafter encounters) on the study area, and spatial distribution of encounters. We also compared body size (wing length), which in juncos is associated with dominance (Baker & Fox 1978, Ketterson 1979), and body mass, presumably an indicator of condition. In spring of one of the years, when we were present before yearlings acquired territories, we analysed first-encounter dates as an estimate of arrival date, again seeking a possible prior residence effect. We also measured body mass at first capture. In spring of the second year, we focused only on territorial yearlings, analysing what we knew of their histories. Finally, in both years we related the locations of territories to locations where we had encountered the birds in the year they hatched. In spring 1989 we implanted some of our subjects with testosterone, but this had no effect on their territorial success.

METHODS

Study area, dates

Our study area in the Appalachian Mountains of the southeastern United States is the Mountain Lake Biological Station of the University of Virginia and adjoining tracts (37° 22' N, 80° 32' W; about 1160 m above sea level). The mountainous topography constrains us to spend most of our time near roads, trails, and dwellings. The maximum distance between locations at opposite ends of it is about 5.3 km. In winter we sometimes catch juncos at lower elevations; birds banded on the study area have been caught about 8 km distant from it.

Dates of field work were 1 May - 8 August 1988; 29 November 1988 - 24 January 1989; 5 March - 19 August 1989; 2-14 October 1989; and 4 April - 26 August 1990.

Processing birds

AGING, SEXING. Nestlings can be aged but, unless laparotomized, can be sexed only if encountered again later in life. Adults and juveniles differ conspicuously in plumage. Juvenile males tend to have longer wings and more white in the rectrices than fe-

males, and upon completing post-juvenal moult males also are somewhat darker than females. Our sexing of individuals in juvenile plumage is about 95% accurate, as we have learned when we have encountered them again during breeding. After post-juvenal moult, young can be sexed even more accurately than 95% and can be separated from older birds by eye colour (autumn) and by subtle differences in the secondaries (any season).

MEASUREMENTS AND BODY MASS. Wings were measured flattened. We present only wing lengths of newly moulted juveniles measured in summer. Juncos do not undergo prenuptial primary moult.

We weighed birds on Pesola spring balances. Time of day of capture did not vary between territorial and non-territorial males. In analysing body mass we excluded individuals undergoing post-juvenal moult. When we weighed juveniles more than once in summer, we used the maximum value. For yearlings in spring, we analysed mass at time of first capture and excluded values obtained after 15 April.

DISTANCES. For birds encountered at least three times as independent juveniles in summer, we present the distance separating the two sites that were farthest apart. When juncos were also netted in October (1989), we use the distance between the 1989 summer and October sites that were closest together. When relating the location of a male's territory to an encounter site in the preceding year, we measure to the closest such site.

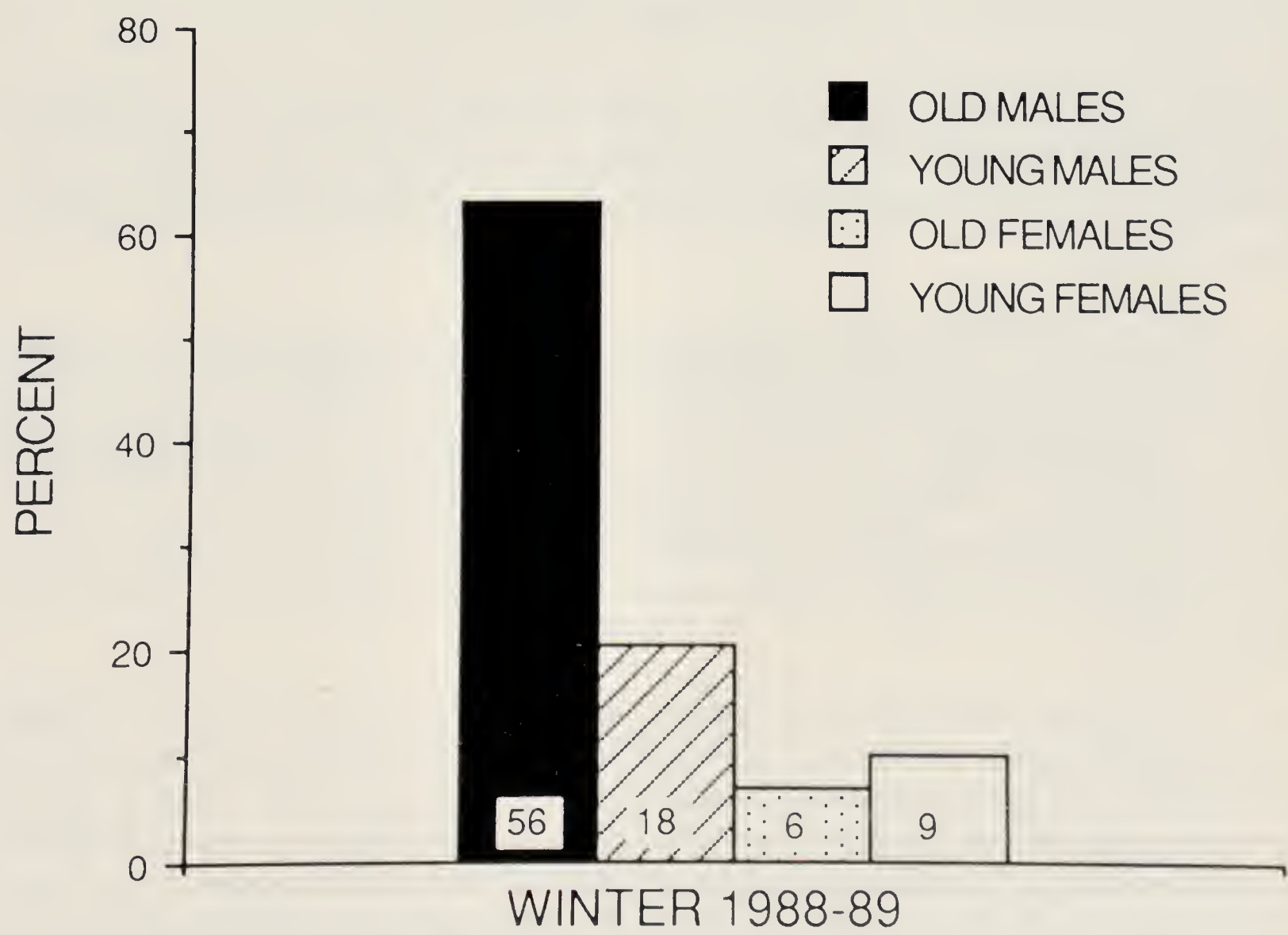


FIGURE 1 - Sex-age structure on study area, winter 1988-89. Sample sizes are enclosed in bars.

ASSIGNMENT OF DATES. We divided the hatching period into May, June, and July, which include probably 95% of all dates of hatching. Hatching dates of young banded as nestlings were known precisely. For birds first encountered as juveniles, we were able to assign many to the month of hatching by drawing on knowledge of the time course of post-juvenal moult. In 1988, the timing of nest predation and the lack of field work in October caused our sample to contain no young males known to have hatched in July, although some certainly did so. In 1989, a spell of severe May weather caused females to interrupt or to postpone nesting, so that our sample contained only one individual from a May nest. In comparing arrival dates of territorial and non-territorial males in 1989, we assign birds among seven-day intervals between 7 March and 1 May, inclusive, in which we first captured them.

General population information

WINTER STRUCTURE. In four winters of study the sex ratio on our area varied between 81% and 86% male (see also Rabenold & Rabenold 1985). In 1988-89, when winter sampling was most systematic and comprehensive, the population was 83% male; of these 24% were young (Table 1). The sex-age classes that are underrepresented on the study area tend to become commoner with decreasing elevation (Table 1). As Figure 1 shows, we have not yet discovered where most old females winter.

REPOPULATION IN SPRING. In late February, juncos that have wintered in flocks off the study area, particularly yearling males, begin to return. In late March, yearling males make up about 50% of the male population (Figure 2). By the end of April, most females have arrived, pairs have formed, and the sex ratio of birds we encounter approaches unity (Figure 3). However, the age ratio among males has fallen from about 50% to about 35% yearlings (Figure 2). This decline in number of yearling males could reflect a nonterritorial surplus of yearlings, or their high April mortality, or an exodus to territories off the study area. All our evidence (including sampling of populations off the study area) points to the first of these possibilities, i.e., the existence of a non-territorial surplus of yearling males on the area, ready to take over territories that become vacant.

SEX RATIO DURING BREEDING. From 1983 through 1986, we removed males to investigate the ability of unassisted females to raise young (Wolf et al. 1990). In 51 of 54 cases (94%) the removed birds were replaced by new males; replacement was quick, often within a few hours. Also, in the few cases when males have disappeared naturally, presumably having died, replacements have quickly taken over their territories. In contrast, when female members of pairs die or disperse to join new mates after nest failure, replacement females usually appear only after several weeks or they do not appear at all.

REPLACEMENT MALES. More than half the replacement males are banded neighbours, some of them unmated, that expand into vacated territories. The remainder, many of them banded, have not previously held territories on the study area, or they are birds that have appeared at several locations on the area, singing for a day or a few days and then moving on. These non-neighbour replacements we consider to be floaters. In our removal study they rarely cared for their predecessors' young (Wolf et al. 1990) but usually paired with the resident female if she nested again. They returned to their newly acquired territories next spring at the normal rate for other territorial males. All non-neighbour replacements that we have been able to age, by their secondaries or

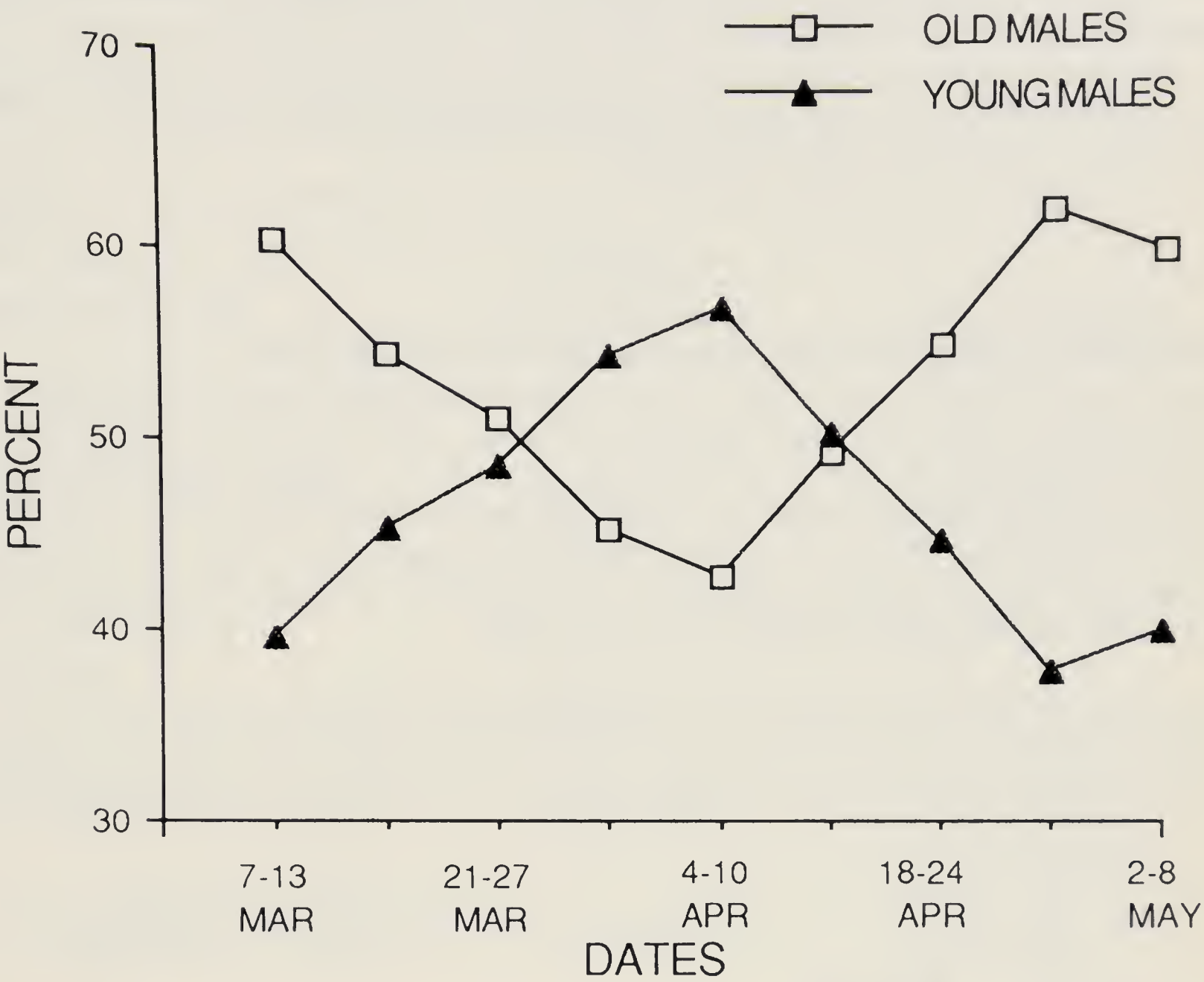


FIGURE 2 - Percentages of yearling males and males older than yearlings caught or, if color-banded, seen at baited sites, according to date, 1989. Total numbers of males per interval, beginning 7-13 March, were 96, 110, 74, 44, 35, 93, 87, and 29. An individual was counted once in each period in which it was encountered.

TABLE 1 - Winter population structure at various altitudes (m), 1988-1989¹.

Altitude above sea level	Males n (%)		Females n (%)	
	Old ²	Young ²	Old ²	Young ²
1200-1160	62 (65)	19 (20)	6 (6)	9 (9)
915-730	43 (49)	16 (18)	10 (11)	19 (22)
670-550	24 (38)	20 (32)	3 (5)	16 (25)

¹ In a log linear analysis, there is no age x sex x altitude interaction ($\chi^2 = 0.10$, df = 2, P = 0.953). Sex and age interact across all altitudes ($\chi^2 = 28.29$, df = 3, P < 0.001); Age and altitude interact across sexes ($\chi^2 = 9.71$, df = 4, P = 0.046); Sex and altitude do not interact across ages ($\chi^2 = 5.86$, df = 4, P = 0.210).

² Old birds hatched in 1987 or earlier, and young hatched during 1988.

(in most cases) because we had banded them as nestlings or juveniles, were yearlings.

DISPERSAL FROM THE STUDY AREA. Some birds that we band as young breed off the study area, as we know from chance encounters.

RESULTS

Attributes of 1989 territorial and non-territorial yearling males

BANDED AND UNBANDED YEARLING MALES, SPRING 1989. We consider first the territorial success of yearling males that we banded on the study area in summer 1988, comparing them with yearlings that were unbanded until 1989. Among 76 already-banded males, 25 (33%) obtained territories in 1989, as against only 5 of 46 (11%) males that we did not band in 1988 (χ^2 , $P < 0.01$). Thus, birds known to have been present when young had greater success next spring. Further analyses compare only the territorial and non-territorial males banded as young in 1988.

HATCHING AND FIRST-ENCOUNTER DATES. In the comparison of 1989 territorial and non-territorial yearlings, the month of hatching in 1988 did not differ (Table 2; χ^2 , $P = 0.621$). There was also no difference in median date of first encounter with these males as

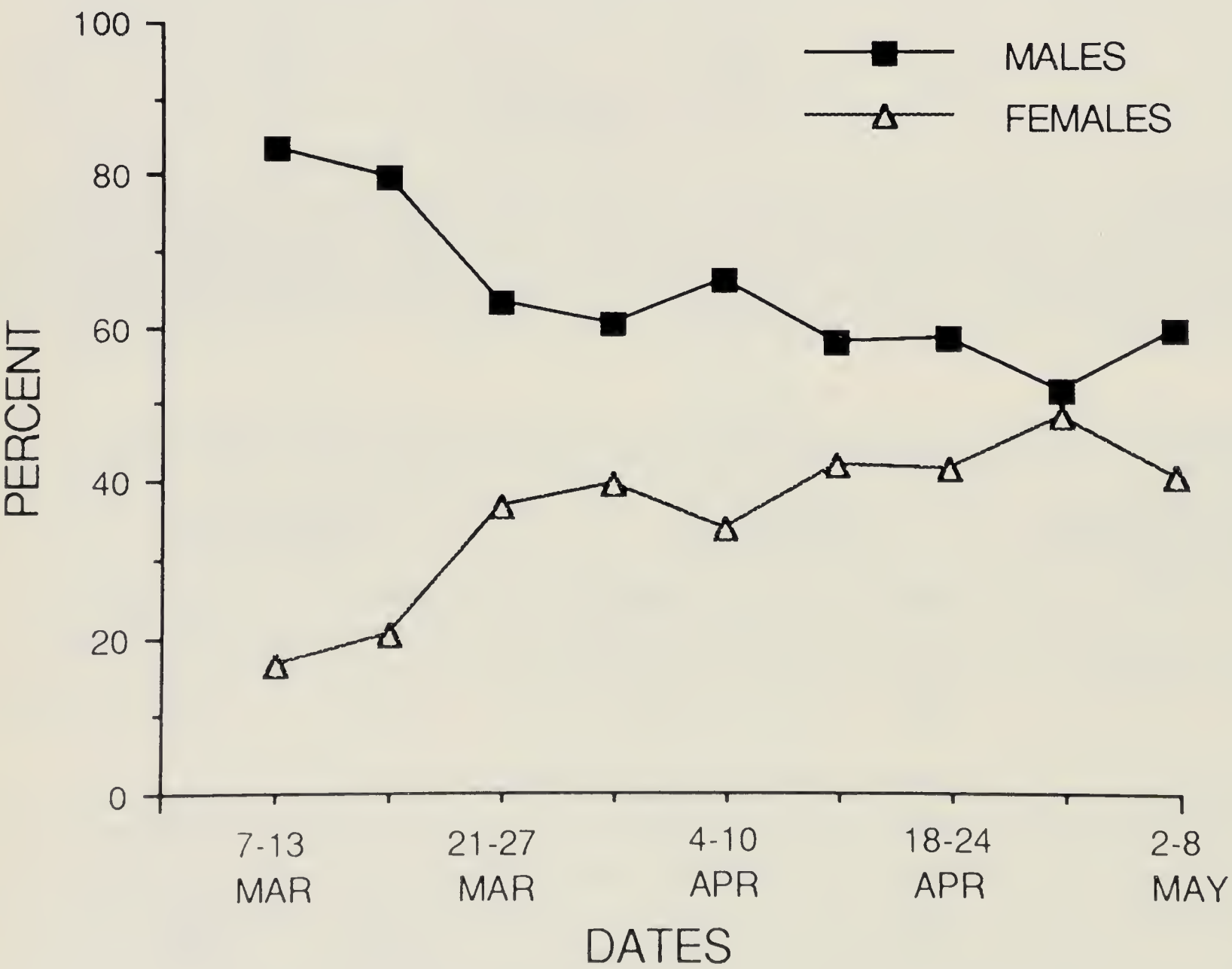


FIGURE 3 - Percentages of males and females caught or, if color banded, seen at baited sites, according to date, 1989. Total numbers of juncos per interval, beginning 7-13 March, were 115, 138, 117, 73, 53, 160, 149, and 56. An individual was counted once in each period in which it was encountered.

juveniles in 1988, including both birds banded in the nest and those of unknown origin banded as juveniles (Table 2; Mann-Whitney U, two-tailed $P = 0.259$). Note a slight tendency for hatching and first capture of non-territorial males to have been earlier instead of later than for territorial males.

TABLE 2 - Characteristics of 1989 territorial and non-territorial yearlings banded in 1988.

Hatching date 1988 ¹	Territorial males	Non-territorial males
May (n)	14	24
June (n)	11	16
First capture 1988, median	20 July (n = 25) ²	18.5 July (n = 51) ²
Summer encounters 1988		
median frequency	3.0	2.5
extremes	1-8 (n = 24) ²	1-7 (n = 50) ²
Distance (m) between summer encounters 1988 (x ± SD) ³	626.3 ± 454.4 (n = 8) ²	798.3 ± 729.4 (n = 26) ²
Wing length (mm) 1988, (x ± SD)	83.0 ± 1.31 (n = 25) ^{2,3}	82.8 ± 1.97 (n = 51) ^{2,3}
Body mass (g) 1988 (x ± SD)	21.37 ± 1.00 (n = 25) ^{2,3}	21.16 ± 1.16 (n = 47) ^{2,3}
First encounter 1989, median ³	21-27 March	21-27 March
Body mass (g) spring 1989 (x ± SD) ³	22.4 ± 1.04 (n = 24)	22.6 ± 0.95 (n = 44)

¹ Predation and the schedule of field work prevented detection of July hatchlings.
² Data pertaining to nestlings and dependent juveniles are excluded, unless the birds were also caught and processed as independent juveniles.
³ See Methods.

ENCOUNTERS WITH JUVENILES, SUMMER AND WINTER. We asked whether 1989 territorial males were encountered as independent juveniles more often than non-territorial males in summer 1988 and whether they may have ranged more widely or less widely over the study area. The two groups did not differ in frequency of capture (Table 2; Mann-Whitney U, two-tailed $P = 0.232$). Among males encountered at least three times, territorial (n = 8) and non-territorial (n = 26) males were statistically indistinguishable in maximum distance between encounter sites (Table 2, two-tailed t test, $P = 0.268$) although sites of territorial males tended to be somewhat closer together.

Ten banded males that hatched in 1988 were caught on the study area during winter (after 28 November). Five were present in spring 1989, and two of these acquired territories. The territory of one was about 150 m from a winter encounter site and of the other, about 1 km.

LOCATION OF TERRITORIES OF BANDED YEARLINGS. All but one of eight 1989 territorial yearlings that had been encountered at least three times in summer 1988 included a summer encounter site within its 1989 territory. The exception held a territory only 120 m distant from a summer site.

ENCOUNTERS WITH NON-TERRITORIAL BANDED YEARLINGS. Of the 26 yearlings that were encountered at least three times in 1988 but that did not acquire territories, 15 were caught or seen in spring 1989 at a previous encounter site. Eleven others ranged from 75 m to 3620 m (median 1095 m) from their nearest 1988 site.

WING LENGTH, MASS. Mean wing length of territorial and non-territorial males measured in 1988 as juveniles did not differ (Table 2; two-tailed t test, $P = 0.228$). Body mass of the two classes was also statistically indistinguishable (Table 2; two-tailed t test, $P = 0.221$). Territorial males tended to have slightly longer wings and to be heavier. When body mass was regressed on wing length, the classes were about the same ($r^2 = 0.002$, $P > 0.5$).

DATE OF FIRST ENCOUNTER, SPRING 1989. Among both territorial and non-territorial males, 58% were encountered in the first two capture periods (7-20 March). More generally, initial encounters of all individuals in each class were similarly distributed (Table 2; Mann-Whitney U, two-tailed $P = 0.321$).

MASS, SPRING 1989. When first captured, territorial and non-territorial males did not differ in body mass (Table 2; two-tailed t, $P = 0.212$), but non-territorial males were slightly heavier.

Attributes of 1990 territorial yearling males

HATCHING AND FIRST CAPTURE DATES. June was the modal hatching month among young for which the point could be determined, and median first capture date of juveniles was 31 July (Table 3).

SUMMER AND AUTUMN ENCOUNTERS. Among 24 previously banded territorial yearlings in 1990, 18 (75%) had been encountered as juveniles at least three times in summer 1989, at sites separated by a median 181 m (Table 3). Fourteen of these 24 territorial males were encountered in October 1989, five of them at a location they also had occupied in summer. The median separation of seasonal sites was 150 m (Table 3).

AUTUMN ENCOUNTERS, SPRING RETURNS. One hundred and three juvenile males were encountered in October 1989, 42 of them banded during the preceding summer and 61 previously unbanded. Eighteen of the already-banded individuals returned in 1990, compared with 15 of the previously unbanded individuals ($\chi^2 = 3.81$, $P = 0.05$). Assuming 50% overwinter mortality (the approximate rate for adult males and probably an underestimate for young), at least 87% of the calculated already-banded survivors ($n = 21$) from October were present in 1990, as opposed to 48% of the calculated previously unbanded survivors ($n = 31$). Focusing on these returning males, 14 of 18 (78%) from the group banded before October acquired territories, and 9 of 15 (60%) from the group banded in October did so.

NUMBERS OF BANDED AND UNBANDED YEARLINGS, 1990. Among 26 territorial yearling males, 24 had been banded in 1989 and two were unbanded until 1990.

TABLE 3 - Characteristics of 1990 territorial yearlings banded in 1989.

Hatching date 1989	
May	1
June	13
July	4
First capture 1989, median ¹	31 July
Summer encounters 1989 ¹	
median frequency	4
extremes	1-7 (n = 21)
Distance (m) between summer 1989 encounters ²	
median	181
extremes	0-2500 (n = 17)
Present October 1989	14
Distance (m) between summer and October encounters 1989 ²	
median	150
extremes	0-1350 (n = 14)
Wing length (mm) summer 1989 (x ± SD) ²	83.0 ± 1.66 (n = 24)
Body mass (g), summer 1989 (x ± SD) ²	22.10 ± 1.11 (n = 23)

¹ Data pertaining to nestlings and dependent juveniles are excluded, unless the birds were also caught and processed as independent juveniles.

² See Methods.

LOCATIONS OF 1990 TERRITORIES. Of the 14 males observed in both summer and autumn 1989, the five that were encountered at the same sites in both seasons gained territories at those sites next spring. Another was encountered at seasonal sites only 120 m apart and included both in his 1990 territory. Of the remaining eight, the territories of five were nearer an autumn site than a summer site and in four of these cases included the autumn site. The territories of three were nearer (and in one case included) a summer site.

Ten territorial males were encountered in summer 1989 but not in autumn. Among these, two held territories at a summer site; the territories of the others ranged from 50 to 3800 m (median 360 m) distant.

COMPARISON OF 1989 AND 1990 TERRITORIAL MALES. We compare, where possible, the 1989 and 1990 territorial birds (Tables 2 and 3). The groups differed in hatching date for reasons given in Methods. Wing length did not differ (two-tailed t, P > 0.5), nor did body mass (two-tailed t, P > 0.5). The 1990 territorial males tended to have been encountered more frequently than the 1989 males as juveniles in their respective preceding summers (Mann-Whitney U, two-tailed P = 0.111) and tended strongly (Mann-Whitney U, two-tailed P = 0.067) to have been encountered at sites that were closer together.

DISCUSSION

We found no correlation between wing length, probably the best indicator of body size (James 1970), and success in acquiring territory. This result is consistent with the findings of Smith (1988) for the Song Sparrow *Melospiza melodia* and of Hannon & Roland (1970) and K. Martin (pers. comm.) for the Willow Ptarmigan *Lagopus lagopus*. Assuming that body mass reflects condition, there was also no difference between territorial and non-territorial males in summer or early spring condition, which parallels Hannon & Roland's interpretation of their data for the Willow Ptarmigan. On the other hand, whereas we detected no hint that age or date of first capture as a juvenile affected territorial success, Arcese & Smith (1985) found in an island Song Sparrow population that late-hatched individuals are subordinate in summer and more likely to become floaters next spring.

Various authors (e.g. Beletsky & Orians 1987) have suggested that previous experience at a site may be a determinant of success in future contests for territories. Yasukawa (1979) compared male Red-winged Blackbirds *Agelaius phoeniceus* that gained initial breeding territories on his study site with males that were present but that failed to gain territories: significantly more successful individuals than unsuccessful individuals had been caught on the site in the preceding year. Our data too, particularly the comparison of success in 1989 of males banded in summer 1988 and males not banded until 1989, indicate the importance of prior experience. Furthermore, 14 of the 24 summer-banded yearlings that gained territories in 1990 were also encountered during a brief capture effort (by only one person) in October. The territorial boundaries of ten of these males encompassed October sites and in both 1989 and 1990 most territorial yearlings settled on sites they had occupied when young.

We conclude that some young male juncos begin to develop attachment to a potential future breeding area in late summer; the attachment may become stronger and focused more specifically in autumn. The probability is about 0.5 that an old male holding territory on or adjoining the focal site will die before next spring. However, in late summer-autumn flocks, more than one young junco probably begins to become attached to the same site. We do not know how or when competition between males is resolved, but late-autumn departure and early-spring return probably are important to success. Moreover, aggressive behaviour is common in summer and autumn juvenile flocks, and future research should be directed both toward increasing the scale of our data and identifying the participants and the winners of these aggressive encounters.

ACKNOWLEDGMENTS

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**CONCLUDING REMARKS: SOCIAL BEHAVIOUR IN THE
NON-BREEDING SEASON**

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We have sampled social behaviour in the non-breeding season and reproductive success of Great Tits and Siberian Meadow Buntings in Japan, Dark-eyed Juncos in America, Silvereyes in Australia and Tropical House Wrens in Panama to see if we can identify the quality of individuals in these species as manifested in their winter behaviour that influences in significant ways the breeding performances in subsequent seasons. In each case we have identified qualitative differences in the behaviour of birds between those with high and those with low reproductive success. These varied from direct takeover of breeding territories in the Tropical House Wren to more subtle patterns of site attachment and advertisement/defence of territories as seen in other species. It is clear from our findings that the fitness components of behaviour in the non-breeding season include not only survival but also, at least in these species, contribution to reproductive success in the following season. It is thus important to examine the total life-cycle strategy encompassing the behaviour of both breeding and non-breeding seasons when we discuss reproductive success of individual birds.

SYMPOSIUM 20

**ACQUISITION AND FUNCTIONS OF
AVIAN VOCALISATIONS**

Conveners P. F. JENKINS and L. F. BAPTISTA

SYMPOSIUM 20

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INTRODUCTORY REMARKS: ACQUISITION AND FUNCTIONS OF AVIAN VOCALISATIONS

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Passerine song is said to function in mate attraction and/or defence of territory. It is only in recent years that ornithologists have developed experimental techniques to test these hypotheses. One method of testing the functions of oscine song is to devocalize the male by rupturing the interclavicular sac. This renders the subject voiceless for a short period, during which time, as Vicky MacDonald will develop for you, grave consequences result for the male Seaside Sparrow, her study species, with regard to retention of territory and acquisition and retention of mates.

Passerine song is also said to function as an ethological isolating mechanism between species. However, with perhaps the exception of the viduine finches, no good evidence exists indicating that song indeed serves as the primary cue in mate selection. The song of the Zebra Finch, unlike the song of the Seaside Sparrow, is entirely sexual in function; and insular Timor and mainland Australian finches mate positively assortatively in captivity. Using song playback and experiments involving males disguised with paint to resemble allospecifics, Nicky Clayton will demonstrate for us that both song and visual cues are important in mate choice.

Charles Darwin first pointed out that song may be the product of sexual selection. Some experimental evidence now exists indicating that females, e.g. in some *Acrocephalus* warblers, do prefer males singing more elaborate songs over those producing simpler utterances. Song complexity may be achieved by learning syllables from conspecific neighbours, or by learning motifs from other species as in songs of some Bower Birds or Starlings. In today's talk, Martine Adret-Hausberger and Peter Jenkins will examine Starling song in relation to intrasexual and intersexual selection.

A large body of literature now exists on the structure and function of song; however, little attention has been paid to the simpler vocalisations of the avian repertoire, namely, the calls. Begging calls of nestlings appear to be the products of opposing forces selecting for the need to be locatable by the parents and the need to be cryptic to avoid predator detection. Ian McLean and Janine Griffin will discuss the possible structure and function of begging calls, asking if begging calls have been shaped by selection for minimum attenuation over distance in specific habitats.

**CULTURAL TRANSMISSION OF BIRD SONG VOCALIZATIONS:
A POPULATION MEMETIC APPROACH**

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ABSTRACT. A new method of analysis of geographic differentiation in bird song that takes into account most of the complexities in the transmission of this cultural trait is developed. This method identifies linked sequences of syllables called memes which are capable of being transmitted within and among populations. Patterns of differentiation within and among populations in New Zealand and Europe, together with some transfer experiments, have allowed us to make inferences about the roles of mutation, migration, drift and selection of song memes across geography. Geographic structuring of Chaffinch song can be explained by these processes operating on apparently neutral memes.

EXPERIMENTAL MANIPULATION OF SINGING RATE AND ITS EFFECT ON CONSPECIFICS

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ABSTRACT. The function of song in a Florida population of Scott's Seaside Sparrows *Ammodramus maritimus peninsulae* was investigated experimentally by temporarily muting male birds in the field. Birds were muted by rupturing the interclavicular air sac. Birds remained songless for about 2 weeks but gave all of their normal calls during this time. Two rounds of mutings were administered, each preceded and followed by time budget, playback, and other observations on three treatment groups: Muted, Sham-operated, and Undisturbed birds. The Early muting round tested for mate and territory acquisition. These Muted birds remained mateless while unable to sing, but most attracted a female after song recovery. The Early Muted birds also acquired territories later than Sham-operated and Undisturbed birds. The Mid-Season muting round tested for mate and territory retention, and for changes in behaviour due to being rendered songless. All Muted birds lost their mates; a few attracted new mates when they regained singing ability. Their territories either shrank or were lost, but new territories were established (or the original re-expanded) after song recovery. Muted birds experienced very high intrusion rates; they reacted with more chases, alarm/threat call, and close displays. There were no discernable differences between Sham-operated and Undisturbed birds for any attributes measured. Another second experimental manipulation increased singing rate by implanting testosterone. The nine implanted birds sang more, and five of these gained an additional mate.

Keywords: Singing, song manipulation, mate choice, territory, muting, testosterone implant, Seaside Sparrow, *Ammodramus maritimus*.

INTRODUCTION

Methods of experimentally investigating the function of song in avian field studies fall into three major categories: eliminate singing by removing the bird and replacing it with played-back song; eliminate singing by muting the bird; and increase singing by implanting testosterone. The first, more familiar, approach has routinely been applied in a variety of published playback experiments (e.g. Yasukawa 1981). I have applied the latter two approaches as a part of my graduate and post-graduate work (McDonald 1986) on Scott's Seaside Sparrows *Ammodramus maritimus peninsulae* (American Ornithologists' Union 1983), a non-endangered subspecies that lives in salt marshes along the gulf coast of Florida, a southeastern state in the United States of America.

Scott's Seaside Sparrows are non-migratory. They are monogamous, and the sexes appear similar. About 10% of the males remain bachelors every year; these males sing two to three times as much as mated males. I never detected unmated females. Most males re-establish the same territory from year to year. However, females do not necessarily return to the same territory, and there is no tendency for pairs to re-mate from one year to the next. Food is plentiful and not a limiting factor for the Seaside Sparrows inhabiting this marsh (Post & Greenlaw 1982). Both males and females usually feed on their own territories, but will occasionally feed, unchallenged, off their territories. One striking feature of this bird's biology is the great amount of time that males spend singing monotonously, even after they are mated. Because of the birds' crypticity and tendency to remain low in the dense salt marsh vegetation, I predicted that the most effective intra- and inter-sexual communication should be vocal.

The experimental portion of my research focused on the question: What is the role of the male's song (as separated from calls and displays) in social behaviour? I performed two sets of manipulative experiments which addressed this question. In the first, I eliminated songs by temporarily muting birds in the field. In the second, I increased singing activity by implanting testosterone. The muting experiment has been published previously (McDonald 1989); the second experiment has not been published.

Until my work of several years ago, the approach of muting birds in the field had been reported for only one species, the Red-winged Blackbird *Agelaius phoeniceus*. Red-Winged Blackbirds were permanently muted by sectioning the hypoglossal nerve as reported in classic studies by Peek (1972) and Smith (1976). These researchers found that muted males tended to have higher trespass rates, although there were complications due to respiratory impairment and the anesthesia. In 1979, Smith described a new technique wherein he temporarily muted Red-wings by rupturing the interclavicular air sac membrane. He obtained similar behavioural results. His sample size was unfortunately small, however, and he did not follow the three muted birds through the season.

Complications in interpreting the results of these previous muting experiments include respiratory impairment, an undesirable anesthesia effect, the elimination of calls as well as song, and these experiments were done on a polygynous species.

Preliminary observations on my study population of Seaside Sparrows suggested that male song probably had a "dual function," i.e. mate attraction and territory establishment and defence. My experimental research objective became: Using a large sample size from my well-studied, colour-marked population, perform controlled field experiments testing the dual function of song, by temporarily muting male birds in the field.

METHODS

My salt marsh study site along the Gulf coast of Florida was 5 km NNE of Cedar Key, Levy County. The marsh was gridded alpha-numerically at 25 m intervals. All Seaside Sparrows within the 30-ha core portion were colour-banded. A more complete description of the study site has been published (Post & Greenlaw 1982, McDonald 1986).

The experimental design consisted of administering two rounds of mutings, an Early- and Mid-season. The Early round tested for female attraction and territory acquisition. The Mid-season tested for female retention, and male (that is, intruder) repulsion. For both, I made two types of comparisons: first, I compared groups, that is, the Muted with the Control (Sham-operated) birds, and the Sham-operated with the Undisturbed birds. The second type of comparison noted changes within individual birds, as determined from behaviour observed during the periods Before, During, and After their manipulations. I also did playback experiments, wherein I observed reactions to the song of a conspecific under more controlled testing circumstances. Results were analyzed with appropriate non-parametric statistical tests.

Early in the season, I observed preliminary territory establishment, banded new unmarked birds, and assigned treatment category (Mute, Sham-operated, or

Undisturbed) for all of the approximately 40 males studied each season. All of the Mid-Season manipulated males had mates; some had nests with eggs, but, with one exception, none had nestlings or fledglings when manipulated.

A summary of my temporary muting technique is as follows: Using mist nets, I captured the birds destined for Muting or Sham-operating. I performed quickly the operation in the field, on or near the bird's territory, without using anesthesia (which I had previously determined to be unnecessary and detrimental to the birds' recovery).

I began both the Muting and Sham-operation by parting the feathers between the furculum, swabbing with antiseptic, and making a longitudinal incision about 1 cm long. Using forceps, I spread connective tissue and exposed the interclavicular air sac membrane. Next, for the Sham-operated treatment, I touched the air sac membrane with a sharp scalpel; for the Muted treatment, I made a small hole in the membrane with the scalpel, and then enlarged it with forceps.

For both treatment categories, I closed the skin with one suture. After swabbing antiseptic and combing the feathers back into place, I carried the bird back to his territory, and released him. The entire procedure, after capture, took less than 15 minutes.

RESULTS

Overview of results of muting experiments

The immediate effects of being rendered songless were these: All but three of the total of 57 manipulated birds were found back on their territories within hours to one day following treatment. One bird died in hand during manipulation, undoubtedly due to the stress of exposure to cold. Two manipulated birds were never seen again, and were presumed to have died. Several weeks later some manipulated birds were recaptured and examined. They showed a small scar, but no infection or other anatomical or physiological consequences were detected as a result of the manipulation. I found no differences in any of the Sham vs. Undisturbed comparisons.

Muted birds tried to sing by going through the motions of singing. They remained songless for about 10-15 days, although by day five they began to utter little squeaks and croaks which gradually became more song-like until they regained their normal individual song. Quite unexpectedly, they gave all of their normal calls.

An overview of the consequences of inability to sing is as follows: The muted birds lost their mates. They suffered immediate intrusions on their territories from neighbours and floaters, and their territories either shrank or were lost as a result. The muted birds tried vigorously to defend their territories, first by attempting to sing more, and then by increasing chasing and close-range displays. After singing ability returned, some of the ex-muted birds regained mates and territory size increased.

Failure to attract/retain mates

In the test of female attraction and retention, not one Early-season Muted bird attracted a female within seven days post-manipulation. In the Mid-season test, only one male retained his mate: she was the mate of the one muted male who had hatchlings. Females simply ignored their muted mates. All mates of muted males left

territories within one or two days; most began soliciting copulations from the nearest persistent singers within a day.

Failure to establish/retain territories

Territory owners normally react to intruders first with increased song activity. If this proves unsuccessful, they intensify aggressive calls and displays given at short range, and chasing. For muted birds, intrusions from neighbours and floaters began immediately, within several hours to a day after muting. Muted mates reacted to intruders first by increasing attempted singing behaviour, and then by intense and aroused calls and close-range displays. Most intruders simply ignored the resident muted bird.

I compared behaviour of muted birds, as measured Before muted and During muted. Intruders were found on muted birds' territories 91% of the total time they were under observation; yet prior to their being rendered songless, these same birds experienced only a 9% intrusion rate. While songless, muted birds spent significantly more time reacting with chases, calls, and close displays than Before. However, muted birds spent less time reacting to intruders with song attempts. Probably this behavioural shift is because the Seaside Sparrow's initial defence behaviour (increased singing directed at intruder) is usually successful. The muted birds' song attempts were ignored; thus they resorted to alternate and heightened defence behaviour.

Perhaps the best overall indicator of how song functions to repel other males is that of territorial integrity, that is, loss of or contraction in territory size. While songless, all of the 21 muted birds' territories were either lost (6), or shrank significantly (15). The average territory size loss was -79%. At the same time, there was an increase in territorial size for both the Sham-operated (+44%) and Undisturbed groups (+31%).

Territorial changes that resulted from the muted birds regaining singing ability showed an opposite trend. Fourteen ex-muted birds expanded their previously shrunken boundaries, and three established new territories.

While their territories were increasing, those of neighbouring Sham-operated and Undisturbed birds shrank by about half. Thus territorial boundaries were plastic, and depended on both the male's current singing ability and his history of territorial occupation or dominance.

What effect did losing singing ability have on the individual's fitness? Obviously, since all muted birds (except one) failed to attract or retain a mate, their fitness dropped to zero immediately after muting. Of those Mid-season Muted birds who obtained a mate after voice recovery late in the season, none produced a successful clutch by the end of the breeding season.

Seeking to determine whether muting had a detrimental effect in subsequent years, I continued my observational studies for four more breeding seasons, from 1985 through 1988. In years following their manipulation, muted birds were no less successful than non-muted birds in establishing territories, obtaining mates, and producing offspring. Indeed, according to the North American Bird Banding Laboratory, the longest-lived Seaside Sparrow on record was one of my experimental, formerly muted birds.

TESTOSTERONE IMPLANT EXPERIMENT: EFFECT OF INCREASED SINGING

Here I summarize an unpublished study conducted in 1987 wherein I sought to determine whether males who spent more time singing were more successful in obtaining larger territories and additional mates. The impetus for this second experiment stemmed from my observations that the former mates of muted birds chose the nearest, most persistently singing male. Unmated male Seaside Sparrows invest greatly in singing, spending two to three times more time singing than mated males, and they continue singing at this high rate throughout the season. Is the improbable benefit of obtaining a female who has deserted her mate worth the cost of maintaining such persistent singing activity? But even those males that obtain a mate continue to sing throughout the breeding season. Although casual observations relating time spent singing to mated status are commonly reported in the ornithological literature (e.g. Krebs et al. 1981), few experimental tests have sought to determine the functional significance of such singing behaviour.

My simple question: Are females attracted to males who sing the most? In other words, is it the quantity of song that appeals to females? Perhaps by having more time to sing, a male advertises his fitness and his territory quality because he can afford the time to sing instead of foraging (Gottlander 1987).

I addressed this question in my study population by monitoring spontaneous song output and correlating it with mate attraction, and also by experimentally manipulating song output. But instead of eliminating song, I increased song by implanting testosterone (T). Testosterone can be effective in increasing song output, but there are complications associated with its use in field studies (Wingfield 1984b, Hegner & Wingfield 1987).

My experimental design structure was similar to the muting experimental design: I compared Testosterone (n = 9) with Placebo (n = 10) and Undisturbed (n = 15) treatment groups; and I compared the testosterone individuals Before and During hormone implantation. Characteristics measured were the following: number of mates, time spent singing, territory size changes, behavioural changes, and physiological changes (plasma T, fat score, and mass). A difference between this design and the muting experiments was that I began these experiments after territory establishment. To more completely address the objective of determining how singing vigour influences female attraction and retention, I used not only the results of manipulations, but also observational data on singing rates from previous years.

Starting in the middle of the breeding season, and continuing until the end of the season, I sampled the blood for testosterone levels in Testosterone, Placebo, and Undisturbed birds. I used placebo tablets, and experimental tablets that released testosterone at a constant rate over 21 days. Tablets were implanted subcutaneously in an apterium along the flank.

In hormone implant studies, it is important to first ascertain whether the implant has been successful in raising the circulating testosterone levels above what is expected for the individual experimental animal. My implants did successfully raise testosterone, as determined by repeated blood sampling. The average T for the Testosterone group was 1.61 ng/ml, compared with 0.73 ng/ml and 0.77 ng/ml for the Placebo and

Undisturbed groups, respectively). Next, I compared the physiological changes in the Testosterone and Placebo groups, and found that over a three week period there were no significant changes in fat or body mass.

With respect to behavioural changes, five of the nine implanted birds gained an additional mate; the implanted birds sang more (62%) and were more active in general; and the territory size increased slightly (8%), but non-significantly.

Singing vigour (measured as time spent singing) was correlated with mate loss, retention, or addition (i.e. polygyny). The small data set from the hormone implant experiment was added to the larger data sets from the muting experiments and from my observations on singing in unmanipulated circumstances (total $n = 98$ territorial males observed at least 10 h per season). All 21 muted birds (except the one described earlier) lost their mates. Five of the nine testosterone-implanted birds who tended to sing at high rates gained an additional mate. Three non-manipulated birds who sang the most also gained an additional mate, while six of the non-manipulated who sang the least lost mates.

Although it may seem advantageous for a male to maintain a high level of testosterone and consequently spend more time singing and gain additional territory size and mates, singing can be costly (e.g. Gottlander 1987, Wingfield 1984a,b). Furthermore, birds implanted with testosterone in this and other studies (e.g. Wingfield 1984a,b, Silverin 1980) were more agonistic and did not provision their young as well as non-manipulated fathers. Over the long-term, male Seaside Sparrows that sing vigorously do not necessarily have a selective advantage over birds with normal and lower testosterone levels.

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THE IMPORTANCE OF PLUMAGE AND SONG FOR ASSORTATIVE MATING IN ZEBRA FINCH SUBSPECIES

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ABSTRACT. There are two subspecies of Zebra Finch, *Taeniopygia guttata guttata* (Lesser Sunda Islands, Indonesia) and *T. g. castanotis* (Australia), which are geographically isolated and differ both in plumage and song. Despite large subspecies differences, there is little geographic variation within island populations of *guttata*. In song playback experiments, females prefer songs of males of their own subspecies. In tests of mate choice and pair formation *guttata* and *castanotis* prefer individuals of their own subspecies. However, *guttata* males that have been painted to resemble *castanotis* males were preferred by *castanotis* females over unpainted *guttata* males; *guttata* females preferred unpainted *guttata* males. In aviaries, the painted *guttata* males paired with *castanotis* females and the unpainted *guttata* males paired with *guttata* females. These results suggest that plumage and song are important for assortative mating between the subspecies in captivity. Birds that were cross-fostered to the other subspecies had songs and plumage that were typical of their own subspecies. However, these birds preferred members of the foster-subspecies in mate choice tests and females preferred the songs of the foster-subspecies. This suggests that learning is unimportant in the development of subspecies differences in plumage and song but that sexual preferences are learnt.

INTRODUCTION

An emerging question in ethology concerns the relationship between the development and function of behaviour. One aspect of this which is of great interest is mate choice. In many species the female is the “choosy sex”. There are fitness advantages in selecting a conspecific mate, but the crucial question is, which male features does a female use for species recognition?

This paper will address this question in the Zebra Finch *Taeniopygia guttata*. Four issues will be discussed. First, I shall consider the differences between the two subspecies *T. g. guttata* (Vieillot) and *T. g. castanotis* (Gould), notably in size, plumage and vocalizations, which might be involved in subspecies recognition. Secondly, I shall describe some experiments which demonstrate that females prefer and recognise males of their own subspecies on the basis of song and that subspecies differences in male plumage characteristics can also be used by females in choosing their mates, leading to assortative mating between *guttata* and *castanotis*. The third issue is a development and function of assortative mating between the two subspecies by considering the relationship between the development of subspecies recognition in Zebra Finches and the function of sexual preferences for members of their own subspecies.

The Zebra Finch is a particularly good species for studying these questions for three reasons. The two subspecies differ in their geographic distribution in the wild: *guttata* occur only on the Lesser Sunda Islands in Indonesia whereas *castanotis* are found on the Australian mainland, 400 km to the southwest. In captivity the birds can

produce fertile, viable hybrids, whose offspring can reproduce (Clayton, personal observation). Nonetheless, when captive colonies of the two subspecies are housed together in aviaries, *guttata* and *castanotis* mate assortatively, i.e. they show a significant tendency to pair with members of their own subspecies (Bohner et al. 1984, Clayton 1990). This suggests that behavioural differences between the two subspecies in their sexual preferences could, at least potentially, effect assortative mating, leading to total reproductive isolation, and thus speciation, between *guttata* and *castanotis* (Mayr 1963, 1970).

A second advantage of working with Zebra Finches is that the two subspecies have remarkably similar breeding ecologies and behaviour but show discrete, quantitative differences in their size, plumage and song. This means that each parameter can be varied in turn to assess which of these potential cues might play a role in assortative mating between the two subspecies. Furthermore, the subspecies differences in plumage (e.g. male breast-band) can be manipulated by painting the birds, providing a verification of the importance of plumage cues. Since the differences between *guttata* and *castanotis* songs could be those which are learnt, it should be possible to obtain birds that visually resemble their own subspecies but sing the songs of the other. This involves the technique of cross-fostering: in this case the young of *guttata*. Using cross-fostered birds, I hoped to be able to ascertain the relative importance of plumage and song for assortative mating between the two subspecies. Sexual preferences in birds are thought to emerge largely as a result of sexual imprinting, the process by which young birds learn (sub)species-specific characteristics that enable them to find a mate of their own subspecies when adult (e.g. Immelmann 1972). By comparing cross-fostered Zebra Finches of both subspecies with those that had been normally raised by members of their own subspecies, I wanted to examine the extent to which both song and mate preferences are influenced by early rearing experience.

The third justification for choosing the Zebra Finch is the simple reason that it is one of the most commonly used species in laboratory studies of the development of both song and mate preferences and it is the only species in which a relationship between the two has been investigated (Clayton 1989a). The practical explanations for this are that the Zebra Finch is widely available, can easily be bred in a small cage, is cheap to feed, readily breeds throughout the year in captivity and has a generation time of about only 90 days.

The Zebra Finch has proved to be an ideal subject for studying behavioural development. The time is now ripe to link what is known about the development of song and mate preferences with their possible function in assortative mating between the two subspecies. The first step in this link is to detail the qualitative and quantitative differences between *guttata* and *castanotis*.

DIFFERENCES BETWEEN *T. G. GUTTATA* AND *T. G. CASTANOTIS*

T. guttata differs from its Australian counterpart, *castanotis*, in being smaller (mean body weight: 9 g *guttata*, 12 g *castanotis*) and *guttata* males also have thinner breast-bands and a grey chin and throat instead of the black and white throat bars. The songs of *guttata* are longer and sung at a higher frequency than those of *castanotis*. In contrast to the substantial differences between the two subspecies, there is little geographic variation within subspecies (Clayton et al. in press).

WHICH CUES ENSURE THAT *GUTTATA* AND *CASTANOTIS* MATE ASSORTATIVELY?

In a recent aviary study of the social interactions and pair formation between members of captive colonies of *guttata* and *castanotis*, two subspecies did not form mixed pairs (Böhner et al. 1984). This raises the important question of which cues ensure that the two subspecies are behaviourally isolated and hence mate assortatively. In song playback experiments, females of both subspecies discriminated between *guttata* and *castanotis* songs, preferring the songs of males of their own subspecies (Clayton & Prove 1989; Figure 1). In multiple mate choice tests and observations of the same individuals during pair formation in aviaries, male and female *guttata* and *castanotis* were found to prefer members of their own subspecies. However, when *guttata* males were painted to resemble *castanotis* males they were preferred by *castanotis* females over unpainted *guttata* males, whereas *guttata* females preferred the unpainted *guttata* males in multiple mate choice tests. In the aviary, the *castanotis* females paired with painted *guttata* males and *guttata* females paired with unpainted *guttata* males (Clayton 1990; Figure 2).

No. copulation displays

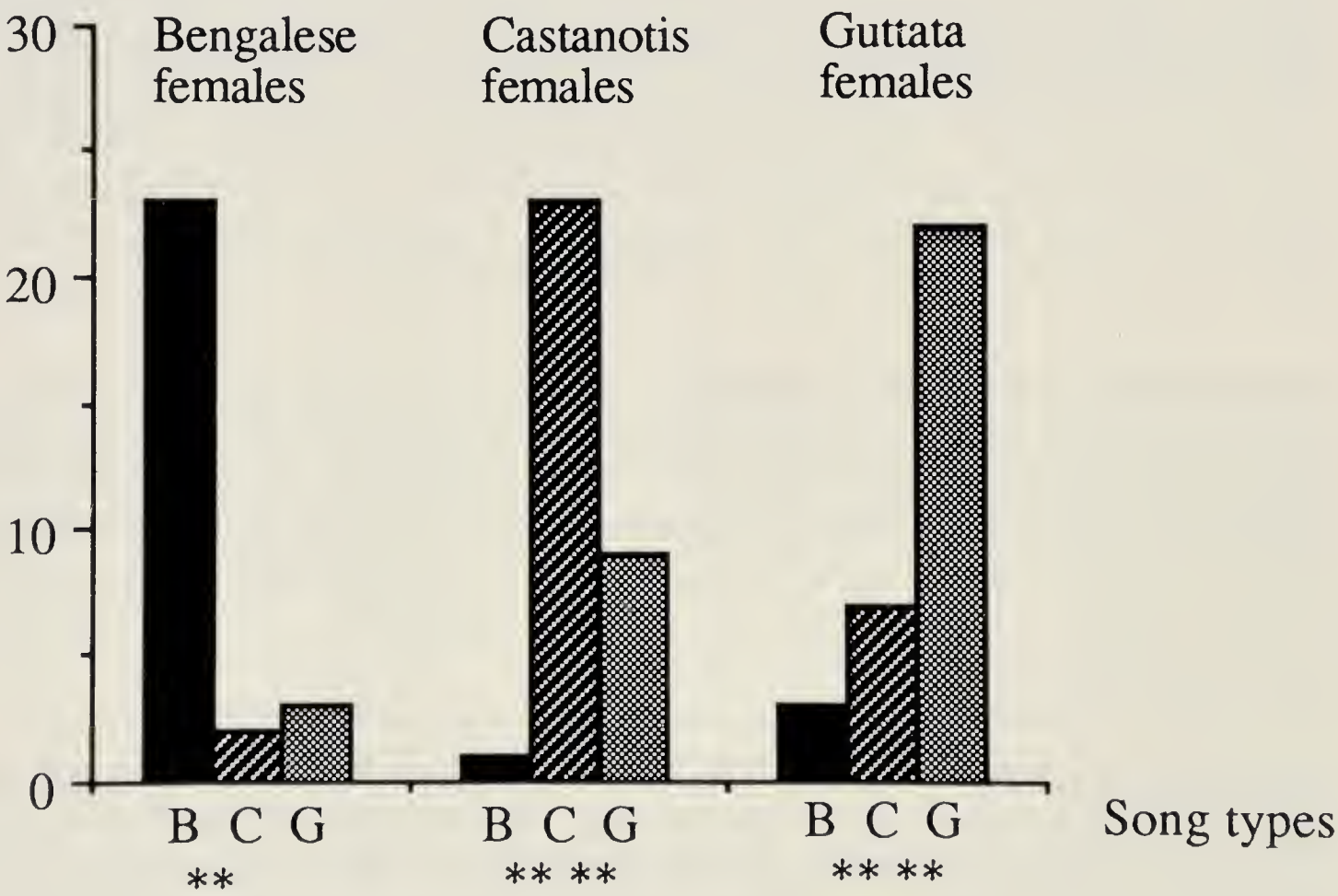


FIGURE 1 – Responses of 25 oestradiol-implanted females (seven Bengalese finches (B), 10 *castanotis* (C) and eight *guttata* (G) Zebra Finches) to playback of recorded song from three Bengalese, three *castanotis* and three *guttata* males. The Bengalese finches served as a species control. The mean number of copulation solicitation displays \pm SD per 12 min song presentation for each group of females are shown. * $P<0.005$, ** $P<0.01$, *** $P<0.001$, Wilcoxon tests having tested for overall heterogeneity with the Friedman ANOVA.

These findings suggest that differences between the two subspecies in both song and breast-band size could play an important role in mate choice and subspecies discrimination, thus leading to assortative mating between the two subspecies in captivity. To assess the importance of early rearing experience on the development of these visual

and vocal differences between the two subspecies and its effect on the development of sexual preferences, *guttata* and *castanotis* that had been cross-fostered to the other subspecies were compared with those that had been normally raised by members of their own subspecies (Figure 3).

		<u>Female</u>	
		<i>Castanotis</i>	<i>Guttata</i>
<u>Male</u>	<i>Castanotis</i>	4	0
	<i>Guttata</i>	0	5

		<u>Female</u>	
		<i>Castanotis</i>	<i>Guttata</i>
<u>Male</u>	<i>P. Guttata</i>	9	1
	<i>UPGuttata</i>	0	9

FIGURE 2 – The number and type of pairs formed in the aviary in each of two groups. (1) Control group: 5 male *guttata*, 5 male *castanotis*, 6 female *guttata* and 4 female *castanotis*. (2) Painted group: 10 unpainted male *guttata* (UPG), 10 painted male *guttata* (PG), 10 female *guttata* and 10 female *castanotis*. Legend as in Figure 1.

WHAT ARE THE EFFECTS OF CROSS-FOSTERING?

Song

When cross-fostered to the other subspecies, *castanotis* and *guttata* males resembled their own subspecies in the macrostructural features of song (e.g. frequency and phrase length) which distinguish the two subspecies' songs. Hybrid males that were raised by one *guttata* and one *castanotis* parent have songs that are intermediate between those of *guttata* and those of *castanotis* males (Figure 4). These results suggest that rearing experience has little, if any, effect on the development of these macrostructural song differences between the two subspecies. In playback experiments, females preferred the songs of their foster-father's subspecies, irrespective of whether the songs were from males that had been cross-fostered or normally raised (Figure 5). This indicates that females use these macrostructural differences in song for subspecies discrimination and that female song preferences are learnt (Clayton in press a).

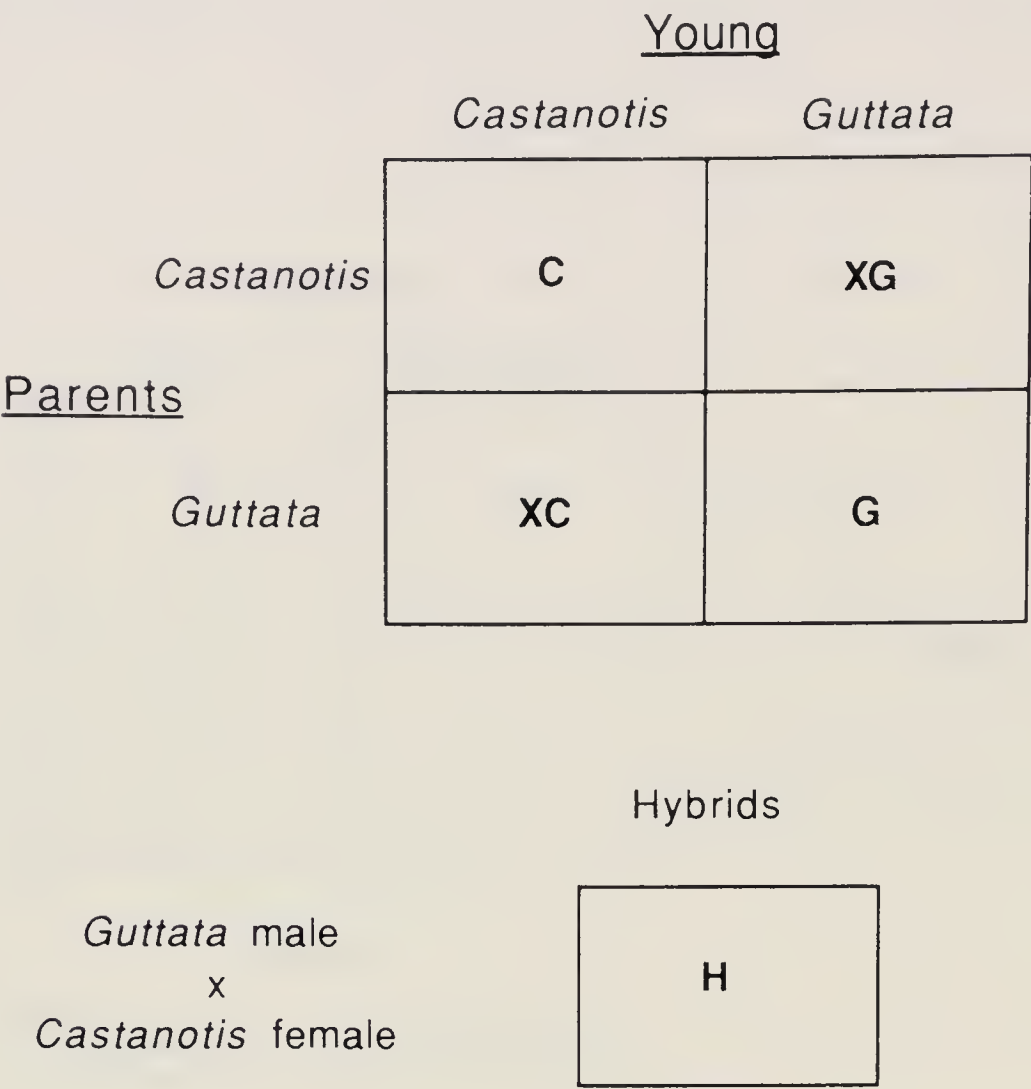


FIGURE 3 – Rearing conditions of the Zebra Finches used in the cross-fostering studies. Normally raised *castanotis* and *guttata* young were raised by a pair of their own subspecies (C₁ & G₁ respectively) in aviaries for 35 days and then housed in single sex groups in cages until day 100 with a different adult pair of the same subspecies (C₂ & G₂ respectively). Cross-fostered *castanotis* (XC) and *guttata* (XG) young were were raised by a pair of the other subspecies (G₁ & C₁ respectively) until day 35 in aviaries and then housed in single sex groups in cages with a different adult pair of the same subspecies as their foster-parents (G₂ & C₂) until day 100. Hybrid young (H1) were raised by *guttata* male and *castanotis* female pairs in aviaries until 35 days of age and then transferred to cages with both sexes of siblings and a different *guttata* male and *castanotis* female pair until day 100.

Plumage

The finding that female Zebra Finches do not discriminate between normally raised and cross-fostered males of their own subspecies on the basis of song raises the question of whether females *can* discriminate between normally raised and cross-fostered males and, if so, which cues they might use. In order to assess which cues females might use it is necessary to consider whether early rearing experience can affect the subspecies differences in size and plumage.

No effect of early rearing experience was found on either size or plumage: cross-fostered Zebra Finches resemble normally raised members of their own subspecies, with hybrids being intermediate. In multiple mate choice tests females preferred normally raised consubspecifics over those that had been cross-fostered and over those of the other subspecies. Since cross-fostered males do not appear to differ from normally raised consubspecifics in plumage, size or song, this result suggests that females discriminate between normally-raised and cross-fostered males of their own subspecies either on the basis of behavioural differences between the two or because the combination of visual and vocal cues improves their powers of discrimination (Clayton in press b)

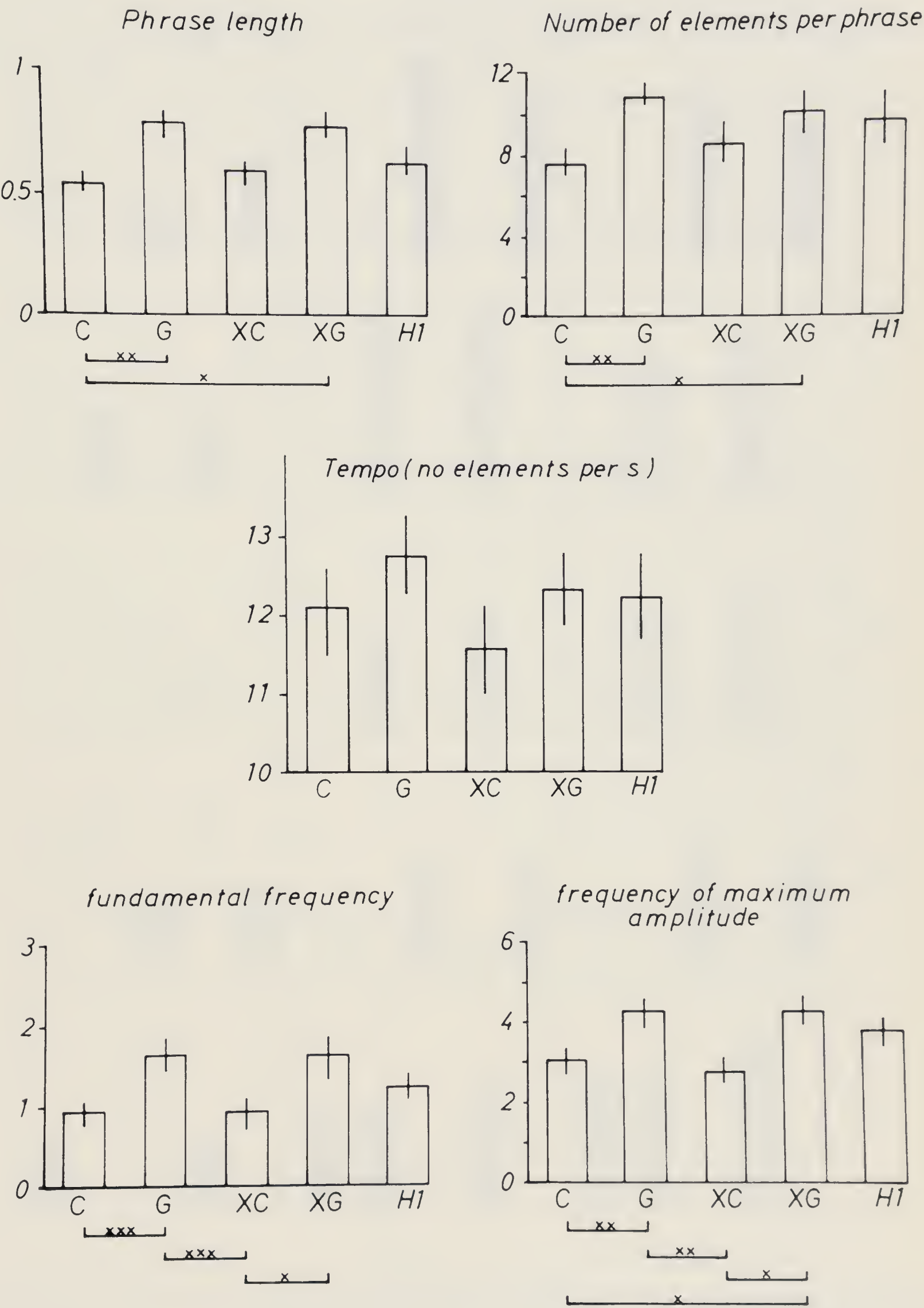


FIGURE 4 – Histograms of mean \pm SD in phrase length in s, in number of elements per phrase, in tempo (number of elements per s), in fundamental frequency (in kHz) and in frequency of maximum amplitude (in kHz). A total of 71 captive Zebra Finches were compared from 18 *castanotis* (C), 18 *guttata* (G), 12 cross-fostered *castanotis* (XC), 12 cross-fostered *guttata* (XG), and 11 hybrids (H1) from *castanotis* female and *guttata* male pairs. * $P<0.05$, ** $P<0.01$, *** $P<0.001$, ANOVA and T tests.

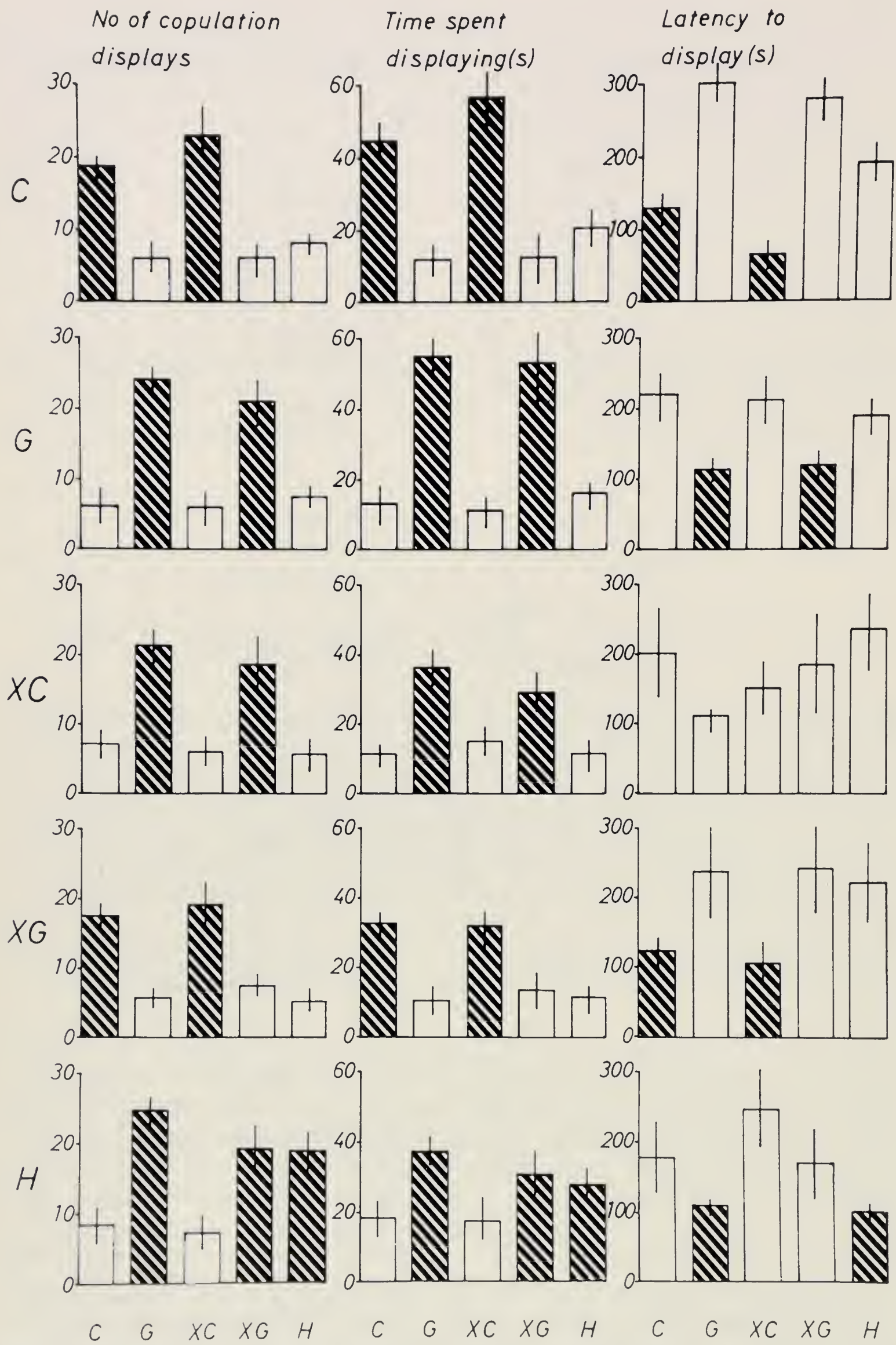


FIGURE 5 – Responses of 54 oestradiol-implanted females (12 C, 12 G, 8 XC, 10 XG, 12 H1) to playback of recorded songs of two C, G, XC, XG and H1 songs from a sample of 50 different songs. The mean number of copulation solicitation displays \pm SD, the total duration of the copulation solicitation display \pm SD, and the latency to respond \pm SD, were calculated per 4 min song presentation for each female group. Stippled bars indicate female preference, i.e. females showed significantly stronger responses to song types indicated by stippled bars ($P < 0.05$ in all cases, $P < 0.001$ in most cases except for latency scores, Friedman ANOVA and Wilcoxon tests). Legend as in Figure 3.

		<u>Female</u>	
		<i>XC</i>	<i>XG</i>
<u>Male</u>	<i>XC</i>	0	9
	<i>XG</i>	1 0	0

		<u>Female</u>	
		<i>C</i>	<i>G</i>
<u>Male</u>	<i>XC</i>	8	0
	<i>XG</i>	0	1 0

		<u>Female</u>	
		<i>XC</i>	<i>XG</i>
<u>Male</u>	<i>C</i>	8	2
	<i>G</i>	1	5

FIGURE 6 – The number and type of pairs formed out of a possible 20 in the aviary in each of three groups. X-X group: Cross-fostered male and female group (10 cross-fostered male *guttata*, 10 cross-fostered male *castanotis*, 10 cross-fostered female *guttata* and 10 cross-fostered female *castanotis*). X-M group: Cross-fostered male, normally raised female group (10 cross-fostered male *guttata*, 10 cross-fostered male *castanotis*, 10 female *guttata* and 10 female *castanotis*). X-F group: Cross-fostered female, normally raised male group (10 male *guttata*, 10 male *castanotis*, 10 cross-fostered female *guttata* and 10 cross-fostered female *castanotis*). X: cross-fostered. C: *castanotis*. G: *guttata*.

Assortative mating

Studies of multiple mate choice and pair formation showed that when both sexes were cross-fostered to the other subspecies mixed pairs (*guttata* - *castanotis*) were formed, suggesting that early experience with the foster parents can have an important influence on pair formation through sexual imprinting on the parents. However, when one sex is normally raised and the other is cross-fostered, the cross-fostered birds usually pair with members of their own subspecies (Clayton in press c; Figure 6). These results indicate that the likelihood of pairing with the “wrong” subspecies is reduced when cross-fostered individuals interact with members of their own subspecies. This would provide an adaptive mechanism for maintaining behavioural isolation between the two subspecies.

LINKING THE DEVELOPMENT AND FUNCTION OF BEHAVIOUR

Mayr (1970) suggested that widely separated allopatric populations may develop pre-mating isolation mechanisms, either by chance or as an incidental result of adaptive changes in other characters in different selective regimes. In support of Mayr's hypothesis, Böhner et al. (1984) and Clayton (1990) have demonstrated assortative mating between two geographically isolated Zebra Finch subspecies in captivity. Mayr (1970) also claimed that “behavioural differences between geographic races do occur but it is rarely known to what extent they have the potential to effect reproductive isolation”. The results presented here (Clayton in press c) suggest that behavioural differences in subspecies preference, which develop through sexual imprinting on the foster parents, could potentially be an important factor in maintaining sexual isolation between *guttata* and *castanotis* in captivity.

In view of the potential role of song and plumage for mate choice it is crucial that females use cues which reliably indicate to which subspecies a particular male belongs. Recent work by Balaban (1988a, b) suggests that female Swamp Sparrows, *Melospiza georgiana*, prefer males that sing their own dialect and that these song preferences are determined by the female's population of origin. It seems likely that Zebra Finches use different rules: females learn to prefer males with certain types of song but the features of song that females use to recognise their own subspecies are not learnt. In both males and females, mate preferences are learnt. As is the case with song features, the plumage cues used in subspecies recognition are also those that are not affected by rearing experience.

Although stereotypy is important for subspecies discrimination, it is generally thought that variety is advantageous for mate choice and territorial defence between conspecifics. In Zebra Finches, learnt microstructural differences in the songs of individuals (e.g. similarity to father's song, Clayton 1987) are thought to influence which male members of their own subspecies females prefer. Selection for song learning may have arisen because errors resulting from the song learning process allow rapid cultural change in song and that such change may confer some advantage to an individual. This hypothesis could also explain why sexual preferences are learnt.

Given the conflict between stereotypy and variety one question which remains is the extent to which the cues used for assortative mating between subspecies are also those used for mate choice within the subspecies. For Zebra Finches, macrostructural

features of song appear to be used for subspecies discrimination whereas the learnt microstructural differences might be more important for mate choice between individual members of the same subspecies. For visual features, it remains to be seen whether females prefer members of their own subspecies on the basis of breast-band size or whether other cues, e.g. bill colour or size, are of more importance.

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SONG CATEGORIES AND THEIR FUNCTIONS IN THE EUROPEAN STARLING

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INTRODUCTION

Very different song structures are frequently observed in the individual repertoires of birds of the same oscine species.

Sometimes song types differ only in detail although extremely dissimilar categories can occur, as for example short stereotyped songs versus long complex ones (Saddleback, Jenkins 1978).

Why evolution has favoured the emergence of such big differences within the one species is far from clear. Catchpole (1987), appealing to Darwin's proposals, suggests that some cases can be explained by the phenomenon of sexual selection. The claim is that conflicts between males require short, loud songs, whereas long complex songs could be attractive to females. In the Reed Warbler *Acrocephalus arundinaceus* he found that short songs are preferentially used in male-male contexts whereas long songs function in female-male encounters. Playback experiments to both males and females support this idea. However too few data on other species are available to be able to understand the role of these song categories in general. In the present paper, we examine these problems in the Starling *Sturnus vulgaris*, a species known for its complex songs and its capacity for mimicry. First we define its song categories including their limits of variability, then we discuss functional aspects in the light of currently available material. Comparison of data from European and New Zealand birds will perhaps enable us to examine the possible universality of the characteristics considered. The Starling is an interesting species in view of its complex social life extending from small breeding colonies to gatherings of many thousands of birds at the night roosts. The breeding system is to some extent flexible, the ratio of polygyny/mogamy varying according to region. The European Starling was introduced into New Zealand about a century ago and is now very widespread and numerous.

MATERIALS AND METHODS

Since the present study consists of a synthesis of data obtained during the course of earlier investigations, we report only briefly the circumstances of the recordings.

Study sites

IN EUROPE. The data used were collected in Germany (Palatinate, Hessen) and in France (Bretagne, Poitou). The songs of about 250 adult males were examined in France between 1979 and 1989. All recordings were made near the nest during the two hours following sunrise (Adret-Hausberger 1983, 1986).

In Germany the populations studied were partially migratory. The songs of 34 adult males were recorded in the Palatinate from April to June 1982 (Adret-Hauseberger & Güttinger 1984). In Hessen a colony of individually banded birds was followed intensively in 1987 and 1988 (Adret-Hausberger et al. 1990).

IN NEW ZEALAND. These starlings are sedentary and nest separately rather than in colonies. Four banded adult males were observed in Auckland successively in 1976, 1977, 1978 and 1980 throughout the year near the nest. Three other individuals were recorded at another site (Papakura) from March to November 1988.

Analysis and equipment

Recordings in Europe were made with Uher 4000, 4200 or 4400 tape-recorders equipped with Sennheiser MD 424 or MKH 416 microphones. Analyses were made using a Kay Sona-Graph model 6061B. In New Zealand Uher 4200 or 4400 tape-recorders were used with a Nakamichi 300 microphone and analysis was carried out on a Kay Sona-Graph DSP 5500.

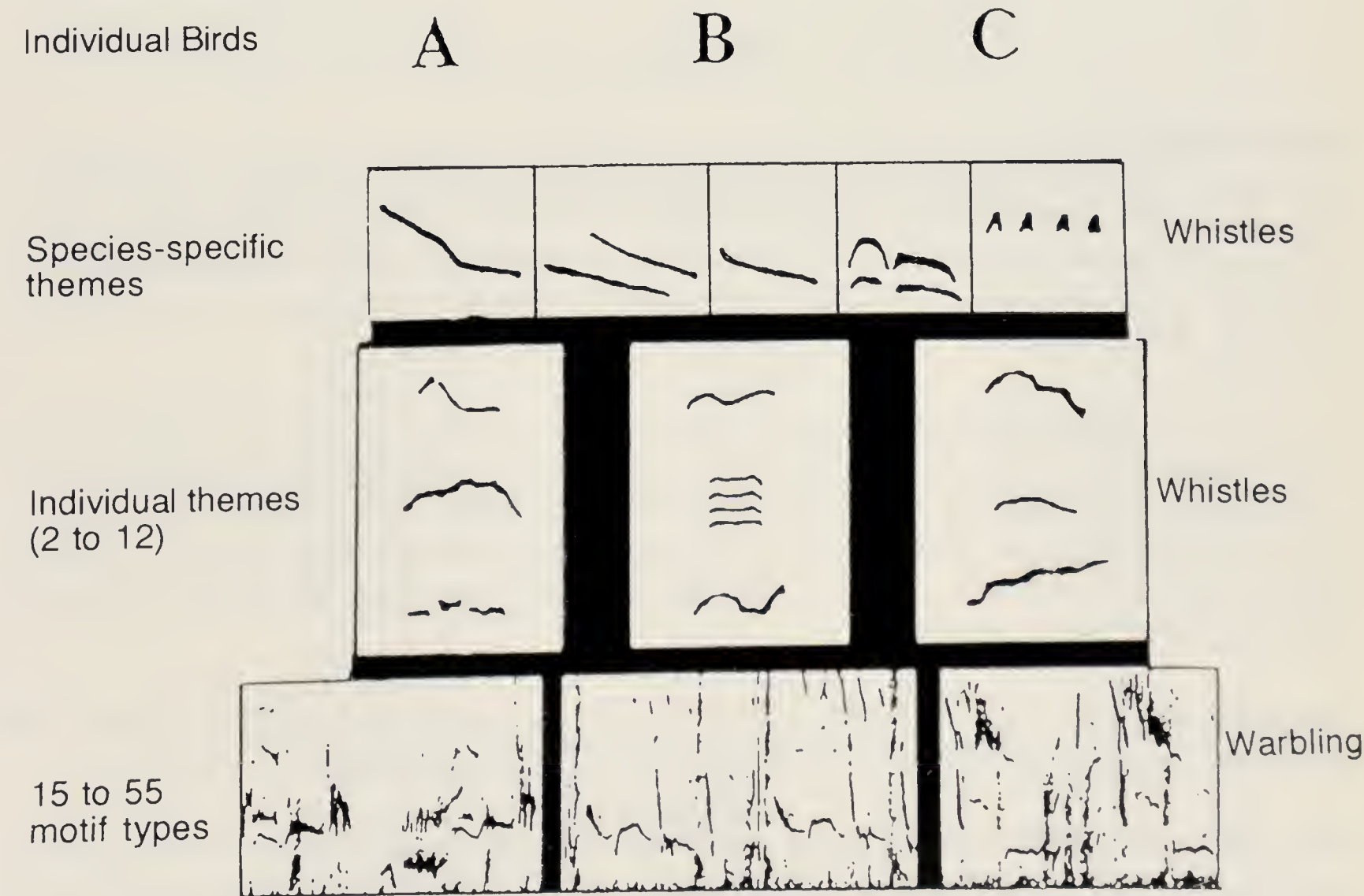


FIGURE 1 – An example of the song structures observed in individual male repertoires.

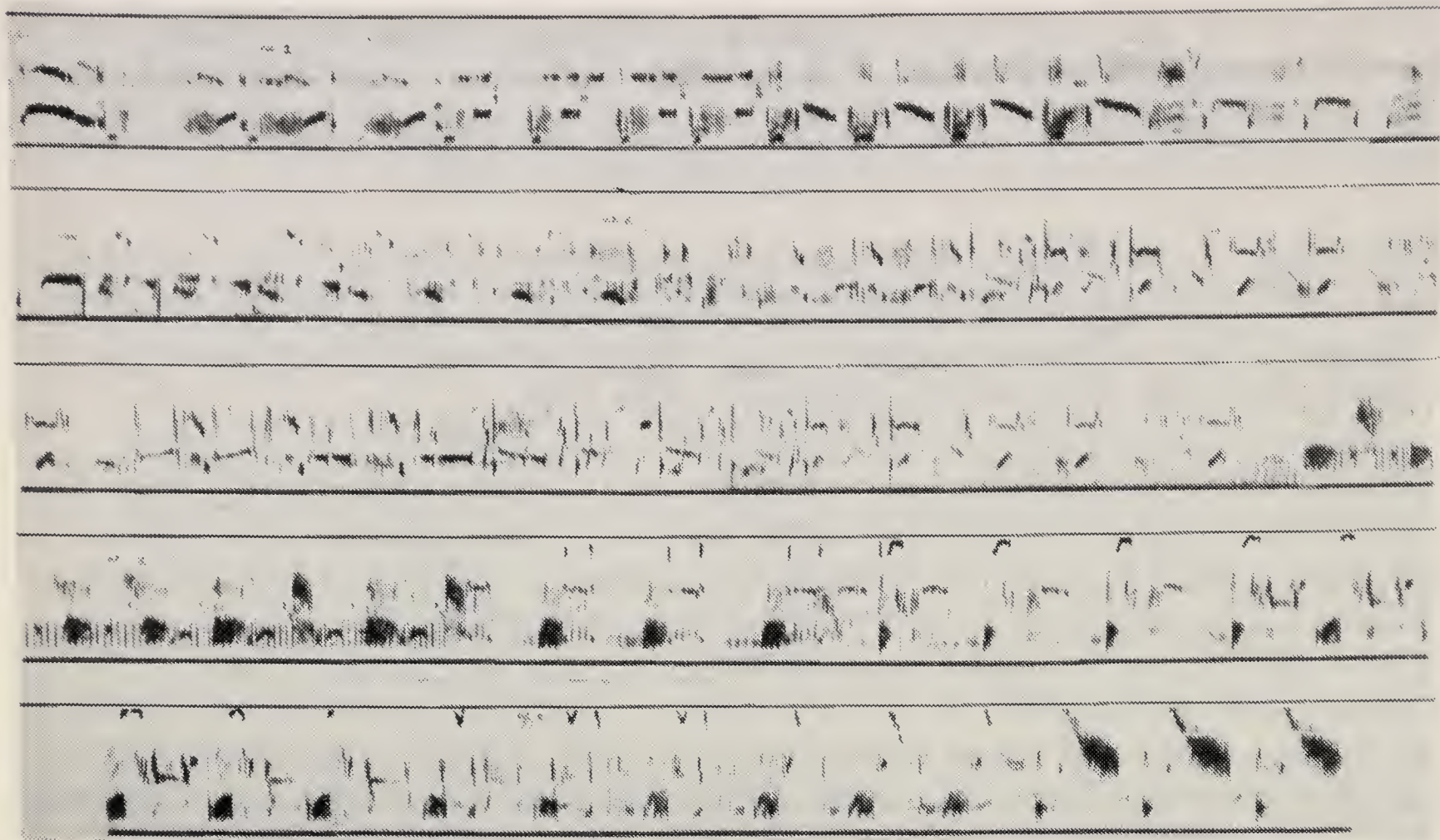


FIGURE 2 – A full warbling sequence sung by a New Zealand bird.

RESULTS

Song categories

INDIVIDUAL RÉPERTOIRE. Using structural criteria we can recognise both in France and New Zealand simple songs consisting mostly of a single note (whistles) and a long complex song made up of very diverse notes arranged in a continuous sequence (variable song) (Figures 1, 2). Both categories of song were found in all adult male Starlings' repertoires.

THE WARBLING SONG. Analysis reveals a very complex structure involving a great variety of notes which follow each other very rapidly, sometimes even one superimposed on another. The notes are not produced independently but are grouped into repeating units called motifs. Motif types are recognizable for their same basic structure either within the one, or in different sequences. Slight variations do appear however from one rendition to another.

The motif repertoire size for A-WR is 26 (from 391 analyses) and for PBI 36 (from 160 analyses). The overall range extends from 17 to 50 for the birds so far studied.

The organisation of the motifs in the warbling sequence is not random in that each is repeated several times before changing to the next, although the number varies from song to song so that two sequences are never absolutely identical. Two motif types are always found at the end of the sequences of both A-WR and PBI. One is composed of clicks combined with low-pitched trills and the second of high-pitched trills (Figure 1). The remaining motifs are individually distinctive even within a breeding colony. The overall organisation of the song is, by contrast, astonishingly similar and this holds for all the other birds investigated (Adret-Hausberger & Jenkins 1988).

TABLE 1 – Loud mimicries obtained in France. The number of individuals singing a given mimicry is indicated.

	Brittany	Poitou
Little Owl <i>Athene noctua</i>	23	5
Buzzard <i>Buteo buteo</i>	22	5
Golden Oriole <i>Oriolus oriolus</i>	6	5
Blackbird <i>Turdus merula</i>	20	5
Lapwing <i>Vanellus vanellus</i>	8	
Black-headed Gull <i>Larus ridibundus</i>	6	
Great Spotted Woodpecker <i>Dendrocopus major</i>	6	
Cat <i>Felis domesticus</i>	3	
Sparrowhawk <i>Accipiter nisus</i>	2	
Redshank <i>Tringa totanus</i>	2	
Curlew <i>Numenius arquata</i>		
flying call	1	
fear		3
Bar-tailed Godwit <i>Limosa lapponica</i>	1	
Trompeter Bullfinch <i>Rhodopechys githaginea</i>	1	
Common Sandpiper <i>Tringa hypoleucos</i>	1	
Squeaking door	1	1
Music	1	
Azure-winged Magpie <i>Cyanopica cyanus</i>	1	
Mistle Thrush <i>Turdus viscivorus</i>		
Nightjar <i>Caprimulgus europaeus</i>		
Song Thrush <i>Turdus philomelos</i>		
Crested Lark <i>Galerida cristata</i>		
White-fronted Goose <i>Anser albifrons</i>		
Herring Gull <i>Larus argentatus</i>		
Number of mimicries recorded	105	24
Number of individual birds considered	80	13

TABLE 2 – Warbled mimicries obtained in Brittany, France. Larger crosses mean that this mimicry was found in the repertoire of more than one bird.

Magpie <i>Pica pica</i>	X
Jackdaw <i>Corvus monedula</i>	X
Moorhen <i>Gallinula chloropus</i>	X
Black-headed Gull <i>Larus ridibundus</i>	+
House sparrow <i>Passer domesticus</i>	X
Swallow <i>Hirundo rustica</i>	X
Batracian sp.	+
Carrion Crow <i>Corvus corone</i>	+
Frog sp.	X
Hen cackling <i>Gallus gallus</i>	X
Blackbird (alarm) <i>Turdus merula</i>	+
Greenfinch <i>Carduelis chloris</i>	+
Partridge <i>Perdix perdix</i>	+
Hammering	+
Water dropping	+
Blue Tit <i>Parus caeruleus</i>	+
Corn Bunting <i>Emberiza calandra</i>	+
Rock Sparrow <i>Petronia petronia</i>	+
Pheasant <i>Phasianus colchicus</i>	+
Goat <i>Capra hircus</i>	+
Goldcrest <i>Regulus regulus</i>	+
Cuckoo <i>Cuculus canorus</i>	+
Coot <i>Fulica atra</i>	
Herring Gull (alarm) <i>Larus argentatus</i>	
Collared Dove <i>Streptopelia decaocto</i>	
Number of individual birds	3

TABLE 3 – Distribution of loud mimicries in New Zealand starlings recorded in two different regions. In some cases, 2 or 3 different calls from one species can be mimicked (example: California Quail).

		Auckland				Papakura		
		AWR	A	B	C	D	E	F
California Quail	1	+	+	+	+	+	+	+
(<i>Lophortyx californicus</i>)	2	+	+	+	+	+	+	+
	3	+	+	+	+	+	+	+
Morepork Owl	1	+			+			
(<i>Ninox novaeseelandiae</i>)	2	+			+			
	3				+			
Red-billed Gull	1	+	+					
(<i>Larus scopulinus</i>)	2	+						
Australian Magpie			+	+	+			
(<i>Gymnorhina hypoleuca</i>)								
Brown Quail		+		+				
(<i>Synoicus ypsilophorus</i>)								
Song Thrush		+						
(<i>Turdus philomelos</i>)								
Blackbird alarm		+		+		+		
(<i>Turdus merula</i>)								
Shepherd's whistle		+	+	+			+	
(<i>Homo sapiens</i>)								
Myna						+	+	+
(<i>Acridotheres tristis</i>)								
Pied Stilt				+		+	+	+
(<i>Himantopus himantopus</i>)								
Oystercatcher						+	+	+
(<i>Haematopus ostralegus</i>)								
Kingfisher	1					+	+	+
(<i>Halcyon sancta</i>)	2						+	
Yellowhammer						+		+
(<i>Emberiza citrinella</i>)								
Rosella	1					+	+	+
(<i>Psephotus eximius</i>)	2						+	
Black-backed Gull						+	+	
(<i>Larus dominicanus</i>)								
Chaffinch								+
(<i>Fringilla coelebs</i>)								
Horse neigh		+	+			+		
(<i>Equus caballus</i>)								
Goldfinch							+	
(<i>Carduelis carduelis</i>)								

WHISTLES. The repertoire of each Starling includes a certain number of highly stereotyped whistle types (17 for A-WR, 9 for PBI) (Hausberger & Guymomarc'h 1981). Within the colony some themes are characteristic of an individual whereas others are common to all members (Figure 2). Indeed these latter ones, the species-specific themes, are found universally in the repertoires of all Starlings with similar characteristics and limits of variability. The individual themes are varied but nevertheless are found with similar forms both in Europe and in New Zealand.

Interspecific mimics and the song categories

In all the starlings observed interspecific mimics are present in both song categories (Figure 3). They may occur as separate loud items in the course of whistled sequences, or may be integrated into the warbling motifs. We have studied the types of mimics occurring in each of these places (Table 1, 2). In Brittany 50% of the individuals sing mimics of only three models - Little Owl, Buzzard and Blackbird. Four other species are frequently mimicked, Oriole, Lapwing and Magpie.

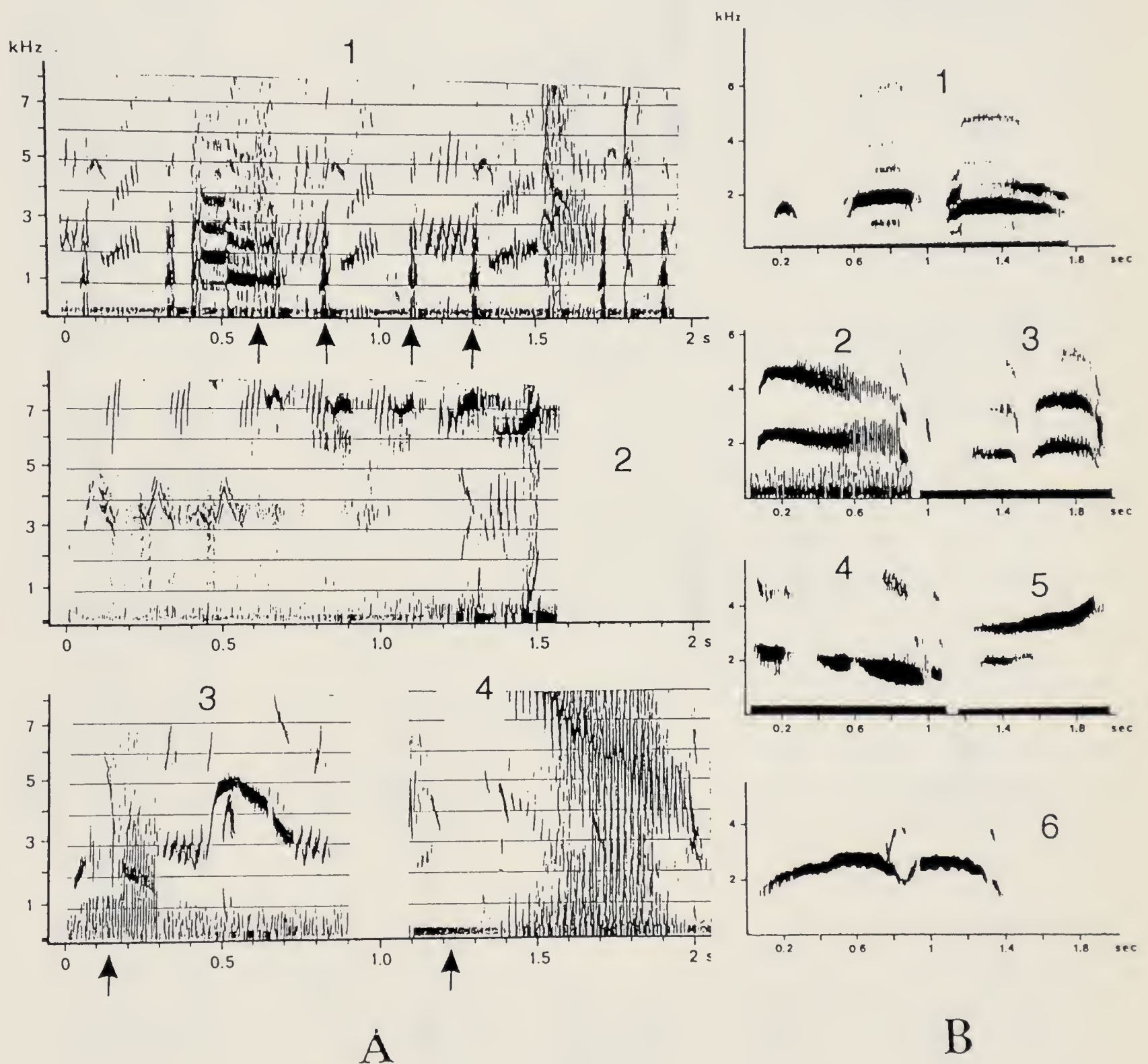


FIGURE 3 – Examples of mimics sung by AWR in New Zealand.

A. Quiet mimics = (1) Hen cackling, (2) Black-backed Gull and Fantail (higher pitched notes), (3) Frog, (4) Duck (low-pitched trill).

B. Loud mimics = (1) California Quail, (2) Pukeko, (3) Brown Quail, (4) Australian Magpie, (5) Shining Cuckoo, (6) Shepherd's whistle.

Similar preference for the same models occurs in other European countries (in prep.). By contrast a wide variety of mimics is found in the warbling song, even within a small sample of individuals. Usually they are the common sounds of the immediate acoustic environment of the bird. Likewise in New Zealand a preference for particular models is observed in the loud mimics (Table 3) even though one of the com-



FIGURE 4 – Species-specific themes and mimicry in whistles: a comparison of the species-specific theme with loud mimicries. A. Species-specific themes recorded in Brittany: (1) 2 variants of the inflexion theme, (2) theme with “harmonics”, (3) simple theme, (4) two examples of the composed theme, (5) two variants of the rhythmic theme. B. Loud mimicries recorded in Europe: (1) Little Owl, (2) Buzzard, (3) Cat, (4) Blackbird, (S) Green Woodpecker, (6) Grey Woodpecker. C. Loud mimicries recorded in New Zealand: (1) Song Thrush, (2) Morepork, (3) Australian Magpie, (4) Brown Quail, (5) California Quail, (6) Kingfisher, (7) Pied Stilt.

monest, the call of the California Quail, is rare at the recording sites. Selection seems also then to be occurring here. In the warbling song, as in France, the preferred models tend to be the common ones in the environment.

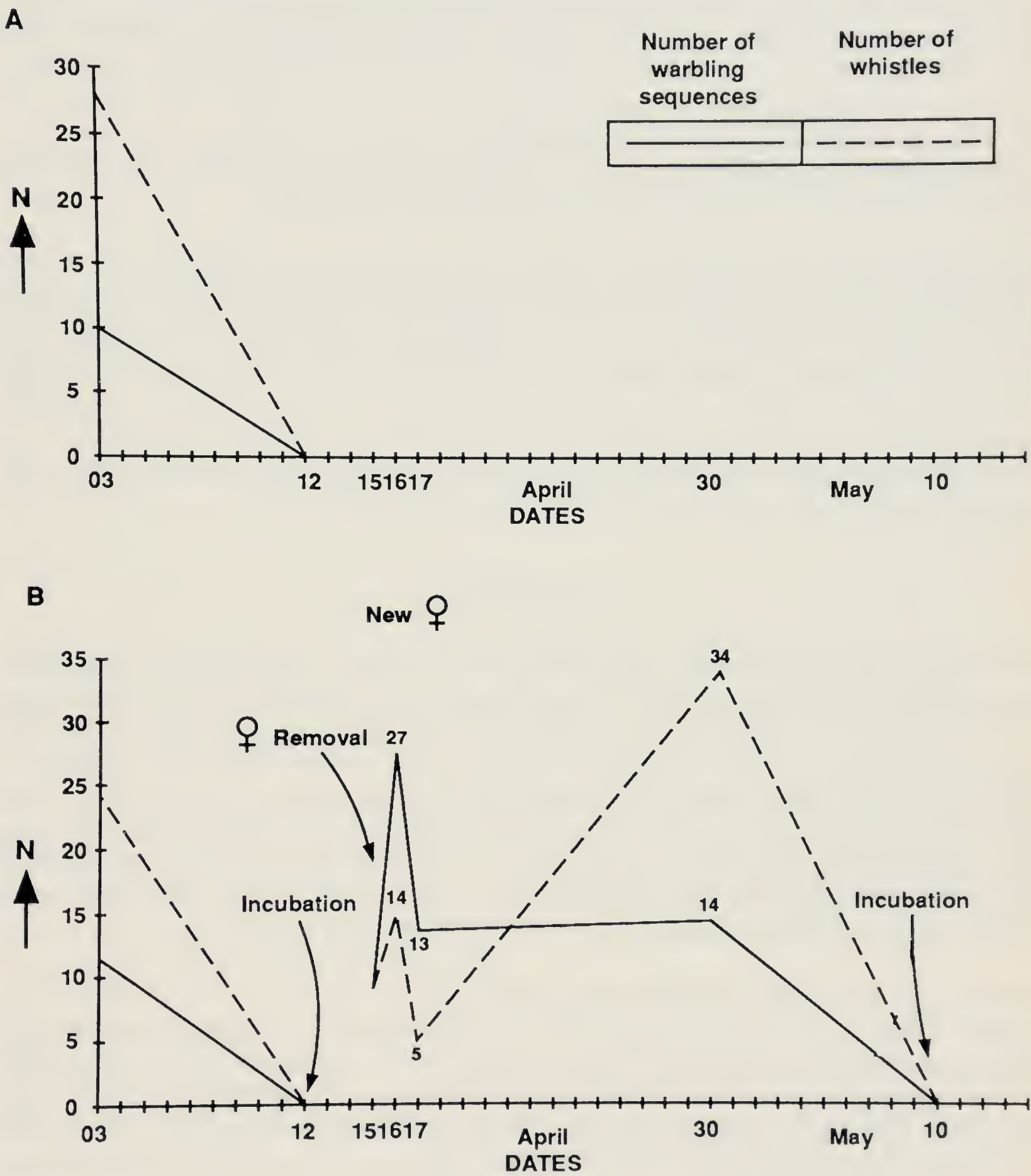


FIGURE 5 – Female removal experiment.
A. Control bird: this male stopped singing when he started incubating.
B. Two experimental males: in both cases, the female was removed at the incubating stage. Both males started singing immediately after her removal.

In both countries there is little overlap between the models used in loud mimicries and those in the warbling song. For example, in New Zealand 80% of the imitations do not overlap and in Brittany none.

The structure of the mimicries tends to match that of their context. The warbling song mimicries are integrated into the motifs where they are interspersed among the other

notes without distorting the specific organisation. As for the loud ones their structure clearly reflects that of the species-specific themes (Figure 4). This is even more remarkable in that the structures preferentially mimicked in Brittany and New Zealand are similar even though the models present in the two countries are very different. This clearly emphasizes that there is selection for particular structures rather than for particular species.

The song categories in the breeding cycle

We investigated the possible variation in the proportion of each song category as a function of breeding status by experimental removal of females.

Males stop singing when incubation commences and they do not sing again until the offspring are ready to fledge at the conclusion of the first breeding attempt, or in the autumn in case of a second brood. However, if the incubating female is removed from the nest during the night, the male starts singing again within an hour after arriving at the nest in the morning. This remains a major activity until incubation is recommenced (Figure 5). However, examination reveals that the two song categories do not vary in the same manner. Warbling predominates largely until pairing with a new female occurs, following which whistles become predominant.

DISCUSSION

The analysis of male Starling songs in Europe and in New Zealand shows the universal existence of individual repertoires consisting of two categories. Each Starling sings unitary whistles of simple form as well as the long complex warbling song. These two can occur independently as for example during vocal interactions (Adret-Hausberger 1982) or in succession. The whistles are highly stereotyped whereas the motifs on which the warbling song is based show slight variations at each repetition. The limits of variability are the same everywhere and some themes are common to all, or almost all, individuals both in Europe and in New Zealand. The warbling song, by contrast, is essentially individual and includes very varied sounds.

Likewise, the interspecific mimics are produced in accordance with the specific categories. They can be sung in the context of whistled songs in a separate and loud fashion, or included in the warbling song. Further, the models copied vary according to the song context. Separate mimics tend to have a simple whistled form and are highly selective as to choice of models. The same few species are mimicked throughout Europe. By contrast varied and complex mimics are found in the warbling song and these tend to reflect the sound environment of the bird.

Preliminary experiments in which the female is removed during incubation show that the proportion of warbling song increases while seeking a fresh mate whereas whistled songs predominate once pair formation has occurred. It is remarkable to find everywhere these two very distinct song categories controlled by totally different rules of organization. What is even more remarkable is that this distinction is found at the level of interspecific mimicry with a clear difference in what is selected to be copied. Starlings appear to be able to learn certain relatively restricted whistled notes which they can modify individually to match those sounds. Moreover selection, in the context of warbling, is based on the organization within the motifs. Given the obvious capacity of this species to produce varied sounds, this canalisation of learning must

be auditory and linked to the existence of two "templates". What we know of song ontogeny suggests that the development of the two song categories is different, the warbling type arising progressively from the basis of subsong, whereas the whistles appear abruptly fully elaborated. In fact, the very structure of the warbling song, its long unbroken sequences and its wide frequency range suggest that it could be a kind of subsong persisting through to the adult stage (Adret-Hausberger 1989). Moreover, new motifs can appear even at an advanced age (Adret-Hausberger et al. 1990). Lanyon (1960) applied the general term "subsong" to all those forms of quiet song found in adults which were long, faint and including diverse mimicries. For Irwin (1988), however, these general features are an indication that subsong is an early stage in development. According to her the simultaneous existence of a primitive stage and of adult song is evidence of paedomorphosis. In fact the retention of subsong could be linked with selection in favour of large repertoires by eliminating crystallisation and permitting the persistence of mimicries. It remains to discover why a species should at the same time have a primitive varied song as well as an adult one.

Catchpole (1982) could have the answer with his hypothesis that, if selection favoured the emergence of long complex songs to attract females, there is a pay-off for a species to have a relatively plastic song into which various items could be integrated. Thus the retention of subsong is one possible mechanism. By contrast male-male interactions, more often than not at a distance, call for simple, stereotyped and loud signals. Some aspects of the song of the Starling do suggest that they have a sexual function. For one thing it is clear that it is the female which chooses the partner and again success in pairing varies greatly from one male to another. Some acquire several females whereas others are monogamous at best.

Our female removal experiment shows that warbling song predominates during the period when a male is seeking to attract a female. Furthermore, polygynous males tend to have a larger repertoire than monogamous ones (Adret-Hausberger et al. 1990, Eens pers. comm.). Finally, copulations solicited by the female are always preceded by warbling song from the male. Mimicries present in the warbling song are very varied and increase its complexity.

The specific whistles are frequently used during vocal interactions between males and their playback provokes a response, which is not the case for warbling song (Adret-Hausberger 1982). They are abundant during "social encounters" whether this be in the colony, in feeding flocks or in night roosts. Preference for the type of whistle used depends on the social context. Individually distinctive whistles allow an observer to immediately recognise at a distance particular birds in a known colony. Individual whistle types often precede warbling sequences (Adret-Hausberger in press) as if to "attract the attention" of a partner before moving on to the warbling type, an elaborate song but of low amplitude.

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STRUCTURE, FUNCTION, AND MIMICRY IN BEGGING CALLS OF PASSERINES AND CUCKOOS

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ABSTRACT. Begging calls given by young birds provide various forms of information, including location and hunger levels, and they stimulate parents to feed the chick. We review the literature on various hypotheses attempting to explain the structure and function of begging calls. A quantitative analysis of the structure of 45 begging calls in relation to habitat supports earlier contentions in the literature that young birds give a remarkable variety of calls, and that there is little evidence for habitat imposed selection on call structures. We argue that the importance of predation as a selection pressure on the location information in nestling calls has been over-emphasised. Rather, we suggest that nestlings do not develop loud begging calls until relatively late in the nestling period, when there is only a narrow window of time left during which they are likely to attract predators. In most species, loud calls given by older nestlings are the same as for fledglings. We suggest that the structure of nestling calls is determined by needs during the fledgling period, when location information is important.

INTRODUCTION

Human beings find it unsurprising that young passerines beg from their parents. After all, birds are highly vocal creatures and we can comprehend the use of a vocal medium for communication. The function of begging calls given by young birds has been taken for granted to the extent that there has been very little study of this apparently important component of parent/offspring communication. The most likely explanation for why chicks call, that calls stimulate the parents to feed the chicks, was demonstrated by von Haartman (1957), and has received little further attention since that time. A further suggestion, that calling communicates hunger level (Collias 1960), has also been accepted without critical analysis. Predation, which is the most likely selective pressure shaping the structure of calls (Lack 1968), has received little experimental attention.

More recently, it has been recognised that call structure is likely to be influenced by transmission characteristics of sound through complex environments (Michelsen 1977, Wiley & Richards 1982). Study of this relationship has been extended to chick vocalisations in only two studies (Redondo & Arias de Reyna 1988a, Popp & Ficken, ms). It seems likely that calls given by young birds have been subject to selection resulting from the interaction between the acoustic sensory apparatus of enemies of birds, and environmental influences on sound transmission. Such a relationship has not yet been demonstrated experimentally.

We begin with the assumption that calls given by young birds are important because they are both incessant and widespread. We know of no passerine bird species whose chicks are known not to call when approached by a parent. Many young birds call incessantly, giving thousands of calls each day. Others restrict their calling to

appropriate contexts (usually the approach of a parent carrying food), but at this time they may be heard from considerable distances.

The aim of this paper is to stimulate thought about the structure and function of begging calls given by young birds. First, we present the results of an analysis of the structure of chick begging calls given by 45 species in relation to habitat. The presentation is necessarily brief due to space limitations. Then we present a prospective discussion, using and expanding on ideas gleaned from the literature.

VOCALISATIONS OF YOUNG BIRDS: METHODS

Tape recordings of young New Zealand birds were made by IGM at Kaikoura, Fiordland, and Little Barrier Island, using a Sony TC-D5M cassette recorder and Nakamichi CM 300 directional microphone. Recordings of northern hemisphere species were obtained from the British Library of Wildlife Sounds (BLOWS). Most of the New Zealand recordings were of young fledglings; most of the BLOWS recordings were of older nestlings. Bird size was estimated using length measures from field guides. The most appropriate measurement, of the weight of the chicks at the age of recording, was not available to us.

All recordings analysed are of temperate zone breeders. There were 41 oscines, one sub-oscine (*Acanthisitta chloris*), and three cuckoos. Each species was assigned as breeding in one of four broad habitat types using notes on the forms received from BLOWS, field guides, bird atlases, and our own personal experience. Habitat classifications were: *open* (nests and lives in low shrubs, savannah, grassland, low cover), *edge* (nests in forest adjacent to open areas where it feeds), *forest* (nests and lives in forest), and *irregular* (impossible to assign to any of the other categories).

Recordings were analysed on a Kay Sona-graph 5500 using the wide band filter. Parameters were measured on the screen for five separate calls chosen randomly from one recording sequence. All measurements are for one brood, although more than one individual may have been measured. Means of the five measurements were used for analysis.

Whenever possible we measured clearly-defined call notes, usually given during low intensity begging. For most notes analysed, adult birds were present nearby but not feeding the chicks. A few of the recordings obtained from BLOWS appeared to be during feeding. Chicks being fed usually call more stridently, often running call notes together into a continuous sequence. Length of call is therefore highly variable and is unlikely to be a useful parameter. Length of call note may also increase as parents approach (McLean & Waas 1987).

Details of measured parameters are given in the Results. Calls were also assigned to one of four subjective call types (pure tone, complex tone, harsh note, buzz; Figure 1). These assignments were made separately by the two authors; disagreements were assigned to one category after discussion.

The frequency containing the highest energy was located by scanning the call note using an amplitude display that sampled across the frequency range (Figure 2).

Where there was no clear strongest frequency, the average frequency of the strongest visual component of the call was used.

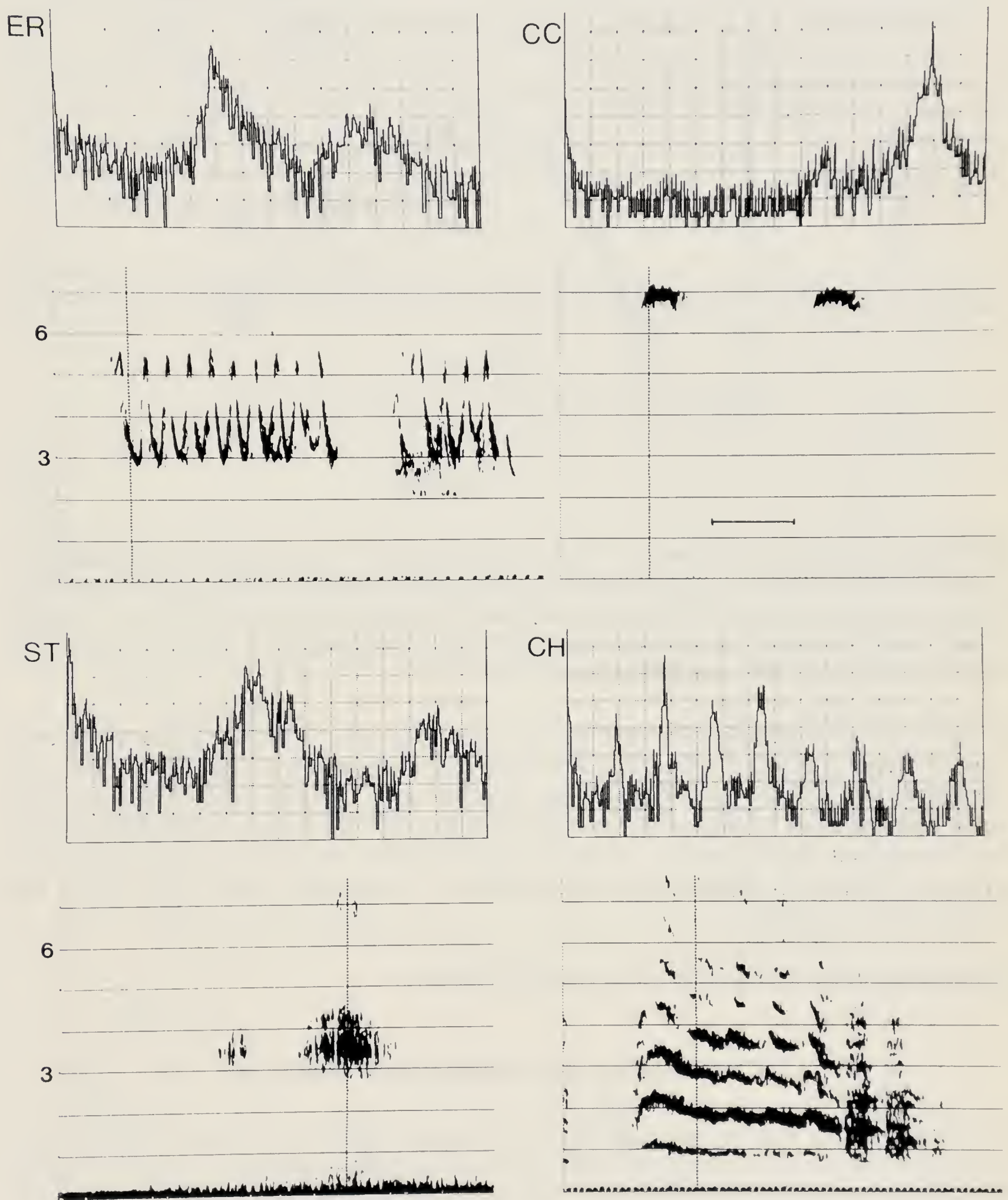


FIGURE 1 – Examples of the four general categories of passerine begging calls used for analysis. Each call is represented as a sonograph (lower) and an amplitude display (upper) taken vertically along the dotted line in the sonograph. The dotted line was placed at the loudest point in the call. Scale on the amplitude Y-axis is arbitrary, measured in decibels. The amplitude X-axis is frequency, as on the Y-axis of the sonograph. Time bar is 0.2 s. ER: "Buzz", *Erithacus rubecula*; CC: "pure tone" *Cuculus canorus*; ST: "Harsh", *Turdus philomelos*; CH: "complex tone", *Pyrrhonorax pyrrhonorax*.

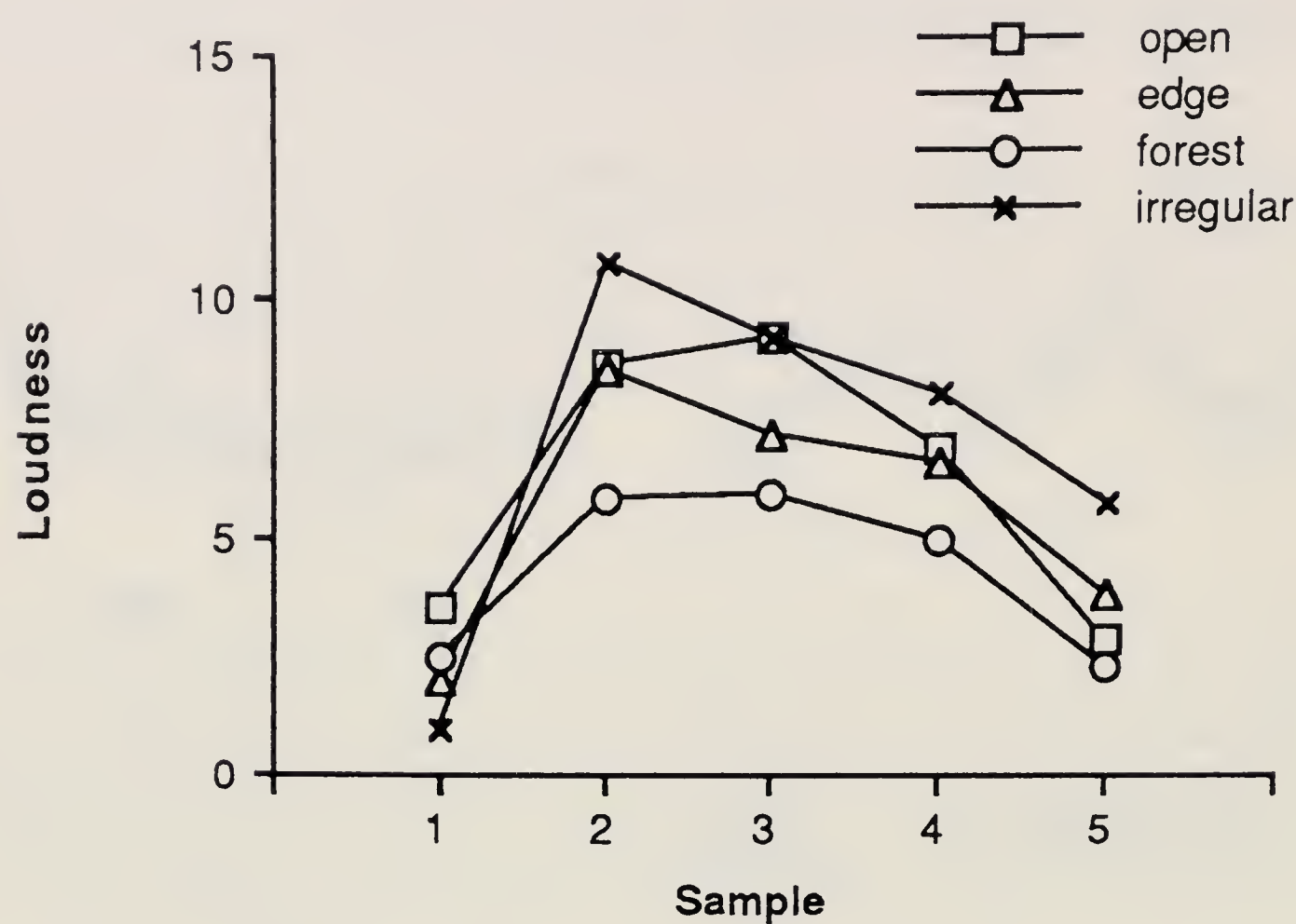


FIGURE 2 – Amplitude structure of chick begging calls in four habitats (see Methods). Loudness is an arbitrary scale; amplitude at five approximately evenly spaced sampling points across the call was standardised so that the quietest sample was set at 1. Sample sizes: open (14), edge (13), forest (14), irregular (4). Error bars are not plotted, but no significant differences among habitats were found.

Amplitude was sampled at five approximately evenly spaced locations along the call. This analysis provides an estimate of the pattern of decibel structure within a call, but absolute loudness cannot be compared between calls. Decibel levels between calls were standardised by setting the quietest sample within a call at 1 db. We scanned for the loudest location in the call as a check to see if any of the five samples approached this value. At least one of them did so in all cases, and in most cases the values were the same.

Statistical analysis was by one or two way ANOVA.

VOCALISATIONS OF YOUNG BIRDS: RESULTS

The three distinct habitat types were equally represented in the data. Only four species were classified as irregular; these were excluded for covariate analyses looking at the effect of habitat and body size. The call types with a tonal structure were more frequently represented than buzz and harsh (Table 1).

Calls of the three cuckoos were classified as pure tone (*Chalcites lucidus*, same as host *Gerygone igata* and call structure similar; *Cuculus canorus*, same as host *Prunella modularis* but call structure different), or harsh (*Clamator glandarius*; different to complex tone classification of host *Pica pica*).

No significant relationship was found between either habitat or call type and any of the measured parameters ($P>0.05$; one-way ANOVAs on: minimum and maximum frequencies and frequency range; main, minimum and maximum frequencies for the component of the call with greatest energy; length of call; d.f. = 3, 41 in all tests).

As expected (see below), call frequencies varied significantly (and negatively) with body size (for frequency of highest energy, $r^2=0.1894$, $t=-3.21$, $P<0.01$). Thus the analysis of habitat in relation to each measurement was repeated, controlling for body size (data from the irregular habitat were excluded from this analysis). Again, no significant relationships were found.

TABLE 1 – Frequency distributions of four call types in each of four habitats. See Methods and Figure 1 for details. SPT: Simple pure tone; CPT: Complex pure tone.

	Call Type				Total
	Buzz	SPT	CPT	Harsh	
Open	1	6	6	1	14
Edge	2	3	5	3	13
Forest	5	3	3	3	14
Irregular	1	1	2	0	4
Total	9	13	16	7	45

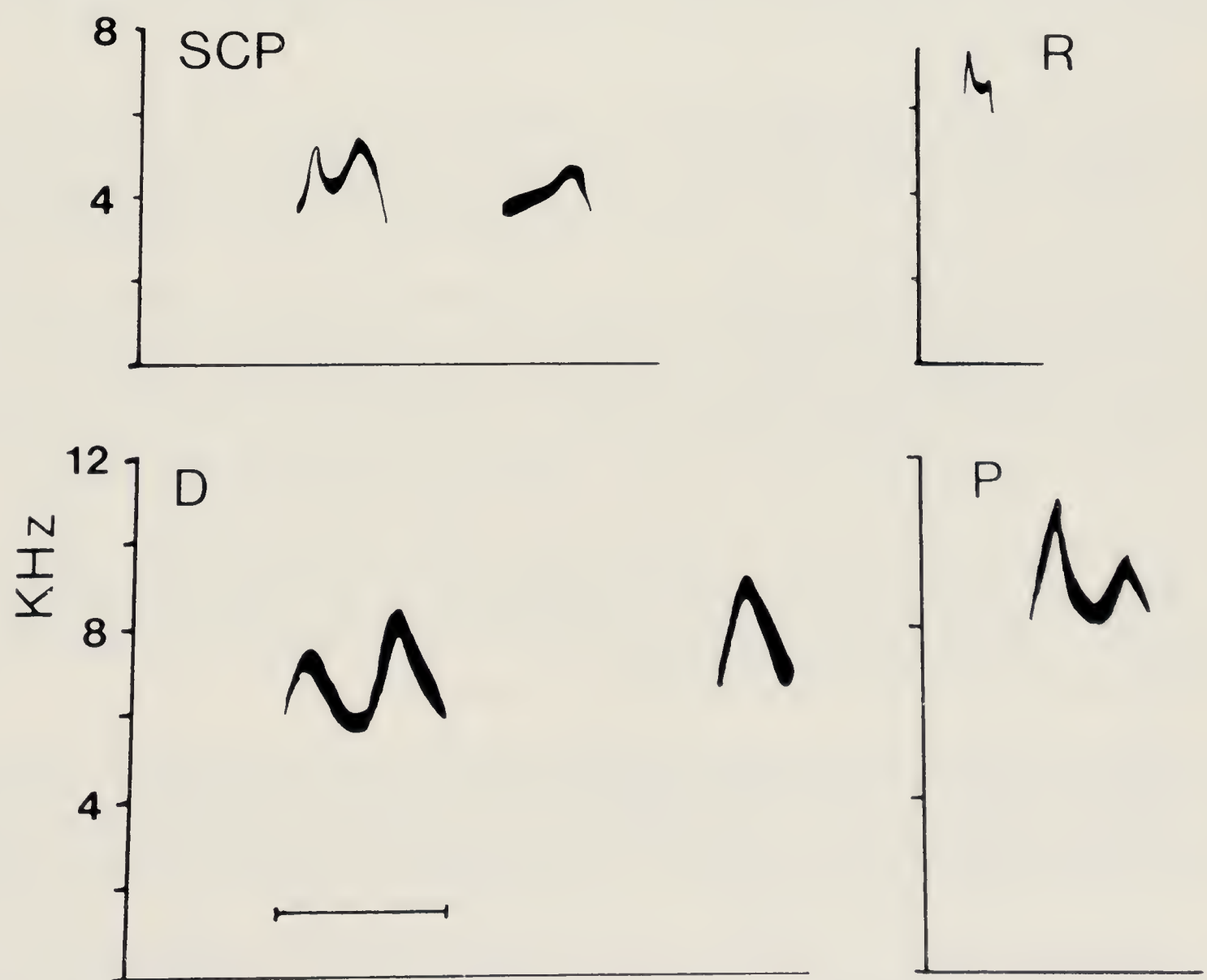


FIGURE 3 – Sonographs of chick begging calls of three passerines (R, *Emberiza schoeniclus*; D, *Prunella modularis*; P, *Anthus antarcticus*), and a penguin (SCP, *Eudyptes robustus*), showing convergence in call structure. Time bar is 0.2 s.

Amplitude structure of the calls was similar across habitats ($F(3,41)=1.22$, NS; Figure 3). Calls were initially quiet, peaked rapidly in volume, then either remained loud or slowly declined, becoming relatively quiet near the end. The three samples in the middle of the calls were significantly louder than the first and last samples but were not significantly different from each other (Duncans multiple range tests). The interaction between habitat and amplitude profile was not significant ($F(12, 164) = 1.28$, NS).

SUGGESTIONS FROM THE LITERATURE

Various trends, suggestions or hypotheses are available from the literature. Here we summarise and develop these.

1. As we also found, there is a negative relationship between call frequency and bird size (larger birds give lower frequency calls; Popp & Ficken ms), a result that has been clearly shown for bird song (Wallschlager 1980). This result is unsurprising, given the physical constraints on a small bird attempting to produce low frequency noise (Wiley & Richards 1982). However, where predation provides a significant selection pressure, young birds may be selected to call at higher frequencies in order to benefit from the poorer directional information provided by such calls (Wiley & Richards 1982, Redondo & Arias de Reyna 1988a). That is, larger birds might be selected to call at the frequencies that small birds are constrained to call at. Alternatively, larger birds may be more effective at preventing predation than smaller birds; thus the selective pressures imposed by predation may be relaxed as bird size increases.

2. Calls of young birds are highly variable. Variation is in purity of sound, overall complexity, duration and frequency. Different populations of the same species may give different calls, and call structure may vary with age (Redondo & Arias de Reyna 1988a) and context (McLean & Waas 1987). Variation with age may be a simple consequence of development; as chicks grow older the sound producing apparatus grows in size and presumably develops in structure. The usual variation with context is in relation to the approach of parents, when chicks tend to beg more stridently. It appears that no simple selection pressure (such as predation) has massaged calls towards a structure common to all passerine species. The reverse may even be true, given the range of calls given by young birds. Although calls are known to change with age of nestlings, we know of no documented case where the chick call changes at the time of fledging – suggestions that this may occur are summarised in Harper (1986). This significant absence appears to have been ignored in discussions of the influence of selection on the structure of chick calls.

3. Calls given by chicks are dissimilar to those given by parents (Redondo & Exposito 1990, Popp & Ficken ms, see Riska 1986 for a non-passerine example). Although adults give the begging calls of chicks in some species (typically females begging from males during courtship feeding, e.g. *Petroica* species, pers. obs.), the situation usually involves either food transfer or dominance in a context where adults mimic juvenile behaviour. Calls given by chicks do not represent a developmental stage in attaining the adult vocal repertoire. They exist for other reasons.

4. Chick calls are likely to have been shaped by context. There are numerous hypotheses and predictions derived from this statement. These include:

- (a) Closely related species living in different habitats or locations might be subject to different sound transmission environments (e.g. closed versus open habitats) or predation pressures (e.g. island versus mainland species). If the young of such species give similar calls, phylogenetic constraints are implicated. Evidence for phylogenetic similarities is conflicting (e.g. species of *Corvus*, *Picoides*, *Spizella*, and *Mohoua* tend to give similar calls, whereas species of *Vireo*, *Sylvia* and *Sialia* do not (Popp & Ficken ms, McLean & Waas 1987).
- (b) Alternatively, young of different species raised in similar habitats should give similar calls if calls have been shaped by context. The most extreme test of this hypothesis is provided by brood parasites and their hosts, particularly cuckoos which have host-specific populations (Payne 1977, Wyllie 1981, Redondo & Arias de Reyna 1988b). There are several suggestions in the literature of cuckoo-host mimicry for chick calls (Courtney 1967, Mundy 1973, McLean & Waas 1987), but to date, too few species have been investigated adequately for any definitive statements to be made. Also, alternative hypotheses to mimicry that may explain the similarities equally well, such as development in the same environment, or chick-parent or sib-sib learning (i.e. learned mimicry rather than evolutionary mimicry) are not usually ruled out (McLean & Waas 1987).
- (c) Suggestions that predation pressures on hole nesting species are relaxed, allowing the development of calls containing more directional information, have provided conflicting results (Redondo & Arias de Reyna 1988a versus Popp & Ficken ms). We suspect that explanation of this discrepancy can be found in the selection pressures imposed once chicks leave the nest, when chicks of hole nesters and open nesters are faced with similar constraints. Redondo & Arias de Reyna (1988a) may also have used younger chicks.
- (d) Chicks of many species exist as dependent fledglings for considerably longer than for the time that they give loud calls as nestlings, despite giving similar calls during both developmental stages. An extreme example is *Mohoua*, where chicks call loudly from the nest for about one week, and are fed by the parents for up to ten months (Gill & McLean 1986).

5. Nestlings develop loud calling relatively rapidly. Chicks of many species give either no calls or extremely quiet, very high-pitched calls, during the first part of the nestling period. Loud calling develops over relatively few days, at about half to two-thirds of the nestling period. These comments are based primarily on anecdotal observations, or indirect statements in the literature; we know of only two studies documenting the amplitude development of nestling calls (Greig-Smith 1980, Knight & Temple 1986). However, it is possible that for many species there is a relatively narrow window of time during which predation pressures are generated by loud calling from the nest.

6. The nest becomes more conspicuous when it contains nestlings (Slagsvold 1982), independently of nestling calls. Parents come and go more often, there is more movement in the nest, and droppings may accumulate around the nest. Predation rates may increase for nests containing older nestlings, but it does not follow that the primary cause is chick vocalisations.

7. At a certain age, usually several days before undisturbed fledging occurs, the response of nestlings to disturbance switches from crouching to “jumping” from the nest. In the Whitehead *Mohoua albicilla*, this switch occurs at 10-11 days of age (McLean & Gill 1988), and is highly correlated with the development of loud chick vocalisations. Undisturbed Whitehead chicks leave the nest at about 18 days. Similarly, undisturbed Common Goldfinch *Spinus tristis* chicks leave the nest some days older than the minimum age at which they can leave the nest and survive (A. Middleton, pers. comm.). We hypothesise that the change in behaviour from crouching to jumping is correlated with the development of loud begging calls in many species, and that many species are capable of leaving the nest up to several days earlier than they normally do. If we are right, the time window during which predators may be attracted to a loud but defenceless basket of babies is reduced even further.

8. Within-nest competition is a potentially significant influence on the intensity of begging by young birds. The development rate of young birds varies to some extent with food intake (Ricklefs 1983), and so selection will favour displays by young birds that (i) increase parental visitation rate overall, and (ii) increase the feeding rate for an individual within the nest at the expense of its siblings. If parents tend to feed the chick giving the most effective display, chicks are likely to use every sensory pathway available to them to attract the parents' attention. McNair & Parker (1979) used two notions: first, that nest predation is a cost shared by all siblings in a nest, and second, that effective begging displays resulting in preferential treatment by the parents result in advantages to individuals; to show theoretically that effective displays are likely to spread through a population even if they result in increased predation at nests. This result was confirmed by Harper (1986).

9. Redondo & Arias de Reyna (1988a) suggest that more locatable calls could evolve under the McNair & Parker (1979) scenario, despite increased costs from predation. We disagree, because their argument relies on the assumption that evolution favours chicks giving more locatable calls within the confines of a nest. It seems unlikely to us that location information could vary significantly on such a small scale. It is more likely that loud calls would be favoured independently of directional quality. A further complication noted by Wiley & Richards (1982) is that in the near field of a sound source, intensity goes through a series of maxima and nulls with increasing distance from the source; for example, the usual inverse square law of sound attenuation does not apply until the receiver is about 1 m from a typical loudspeaker. Although this distance will be smaller for birds, the distances involved for a parent sitting on the edge of a nest may mean that chicks are selected to produce complex sounds that minimise this effect. One of the functions of head waving by young birds may be to ensure that the distance between themselves and the parent is constantly varying so that the parent does not remain in a null zone for long.

However, many chicks clearly do give calls containing good information about location. Calls that give poor location cues are pure notes at a high frequency (Wiley & Richards 1982). In our review we found three species that gave pure-toned calls of very similar structure (Figure 3). All were ground or near ground nesting species, suggesting convergence of call structure. Unfortunately, these calls are virtually identical in structure to the begging peep of the Snares Crested Penguin *Eudyptes robustus* (Figure 3), a species with no predators that could benefit from location cues in chick calls (it breeds in large colonies), and which should have been selected to

give location cues under the Redondo & Arias de Reyna scenario. Parent and chick penguins use the nest site in order to find each other once chicks enter a creche (Proffitt & McLean, in press) and post-fledging location cues are of little value. Although we have no explanation for the apparent convergence in call structure among these four species, we suggest that the answer will not be found in a simple balance between predation pressures and the need to provide information about location.

WHY DO YOUNG BIRDS GIVE BEGGING CALLS?

The energy devoted to begging behaviour, including calling, by young birds, demands a functional explanation. Begging clearly encourages parental feeding rates (von Haartman 1957), and intensity of begging may additionally communicate intensity of hunger (Collias 1960).

However, behaviours such as head waving and wing fluttering, when combined with morphological features such as brightly coloured mouths, mean that chicks have an extensive display repertoire that is likely to stimulate feeding, even without calling. Any additional benefit in increased food intake attributable to calling must be large enough to counter costs resulting from the hypothesised increased conspicuousness of the nest to predators. Alternatively, if calling is an effective attention getting device within the nest, chicks may be constrained to call even if calling is suboptimal behaviour.

We accept that begging calls given in the nest function to provide an additional stimulus to parental feeding. Evolution or development of loud calling may additionally be encouraged by within-nest competition. We disagree that calls given by nestlings are needed to provide location information or communicate hunger. Location information is superfluous for chicks in a nest, and hunger can be communicated in other ways, such as by raising the head highest during begging, a cue that appears to be used by Fantails *Rhipidura fuliginosa* (pers. obs.).

We believe that the supposed influence of predation on call structure of nestlings has been exaggerated, because there is a relatively narrow window of time when chicks calling loudly are susceptible to within-nest predation. Studies of whether predators actually use chick begging calls to locate nests provide conflicting results. Brosset & Chappuis (1968) found that mammalian predators perceived the calls of young birds, but they did not respond to the calls with predatory behaviour. Both Dunn (1977) and Gochfeld (1979) thought that predators used nestling calls to locate nests. It seems likely that, if humans can learn to locate nests using begging calls, predators will also do so.

We suggest that the primary reason that many young birds give loud calls containing good location cues is because they need to do so immediately on leaving the nest. We find it unsurprising that calling is developed while chicks are still in the nest for the reasons outlined above. Developmental factors are also likely to be operating - some practice may be required, and development of the vocal apparatus may require use. Lack of a documented change in call structure at the time of fledging for any species supports our argument.

Once out of the nest, chicks have a wider range of options for avoiding predators, such as cryptic behaviour. An example from our experience is young Song Thrushes

Turdus philomelos, which are easy to hear and locate but are almost impossible to see when in forest habitat.

WHY DO CHICK CALLS VARY IN STRUCTURE?

Perhaps the only generalisation that can be made about chick calls is that they vary tremendously in structure. Marler (1955) contended that chicks gave calls similar to the "aerial predator" call of some adult birds, and that such calls provided little information about location. Some species clearly do give calls that either provide little information about location or attenuate rapidly through a variety of effects outlined in detail in Wiley & Richards (1982). However, it is not clear that these calls occur any more frequently among passerines than calls that provide good information about location. There are sound reasons for providing information about location anyway.

We have identified no general selection pressure likely to be operating on calls given by chicks. As with bird song, chick calls probably have a multitude of functions, with a few functions predominating across species. These include species and possibly individual identification, information about physiological state and location, and reinforcement and/or manipulation of parental behaviour. It therefore becomes unsurprising that chick calls vary in structure.

What can we learn from the calls given by cuckoo chicks? Similarities between begging calls of cuckoos and their hosts (McLean & Waas 1987), and differences between calls of the same cuckoo using different host species (Redondo & Arias de Reyna 1988b), suggest that cuckoos have been selected to mimic the begging calls of their hosts. The lack of convergence in call structure among passerines generally suggests that any apparent mimicry found is true mimicry.

However, passerine birds tend to feed any chick appearing in the nest. The best known example in New Zealand is from the management programme of the Black Robin *Petroica traversi*, chicks of which were raised by two host species *Gerygone albofrontata* and *Petroica macrocephala*. Also, we have shown experimentally that parent Grey Warblers *G. igata* discriminate between the begging calls of their own chicks and those of their host-specific brood parasite, the Shining Bronze Cuckoo (McLean & Rhodes in press). This discrimination is made even when the parent warblers are raising a cuckoo at the time of the test. Despite mimicry in the calls of New Zealand cuckoos, we suspect that cuckoo chicks would be successful if they made any noise at all. Presumably the chicks of Brown-headed Cowbirds *Molothrus ater* do not mimic the calls of the 200+ species they are known to parasitise (Rothstein 1982).

The function(s) of begging calls of passerine birds remains enigmatic, as do the selection pressures operating on them. Due to a lack of selection, young birds may even give calls that appear to be inappropriate. Young New Zealand Kingfishers *Halcyon sancta* give a warning call that mimics a snake hissing (pers. obs.). This call is entirely inappropriate in New Zealand and presumably reflects the species' Australian origins. In this review we have attempted to raise issues that beg further attention, and we suggest some alternative hypotheses to those prevailing in the literature. The diversity of calls given by young birds suggests exciting potential for testing ideas that have already been developed in studies of bird song.

ACKNOWLEDGMENTS

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CONCLUDING REMARKS: ACQUISITION AND FUNCTIONS OF AVIAN VOCALISATIONS

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For many years we have had to be content with accepting the claimed functions of bird song without many examples of rigorous proof of them being available to us. But researchers are now moving into a phase where active intervention in the signal system of a species is being carried out to reveal particular functions. In this symposium, three very diverse interventions are described, temporary silencing of a territorial individual to observe the consequences of vocal signal loss, cross-fostering of eggs so that young grow up in the “wrong” song learning context, and the removal of an incubating female causing the male to revert to the song behaviour of the pairing phase of the breeding cycle.

In the first, the functions of song in the holding of territory and mate were confirmed, in the second the sexual role of song was revealed, and in the third the proportions of warbling to loud song before and after removal confirmed the hypothesised functions of these two song components.

An important spin-off from the cross-fostering experiment was that major species-specific characteristics of song syntax were not modified by the cross-fostering experience, indicating an innate component in macrostructural ontogeny.

In the fourth paper the authors investigate the prediction that convergence would be expected in begging-call structure as appropriate to particular habitats. It is interesting that this proved not to be the case, and that the amplitude profiles in different habitats proved to be remarkably similar.

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CIMPRICH D A	1432	EMMERTON J	1837
CLAYTON N S	1252	ENS B J	889
CLOUT M N	1617	ERIKSTAD K E	2272
COCKREM J F	2092	ESCALANTE-PLIEGO P	333
COLLIER K J	860	ESTRELLA R R	1641
COLLINS B G	1139	EVANS P R	2197
COLLINS B G	1166	EVANS P R	2228
COOKE F	1666	EVANS P R	2236
COOPER A	554	EVANS R M	1734
COULSON J C	2365	FAITH D P	404
CRAIG J L	231	FEDUCCIA A	1930
CRAIG J L	2513	FEINSINGER P	1480
CRAIG J L	2546	FEINSINGER P	1605
CRAIG J L	2553	FIVIZZANI A J	2072
CRAIG J L	2561	FJELDSA J	342
CROWE T	449	FORBES L S	1720
CROWE T	483	FORD H A	826
CROXALL J P	279	FORD H A	1141
CROXALL J P	1393	FORD H A	1470
CULLEN D P	1229	FORD H A	1568
CURRY R L	1333	FRANKE I	317
CUSTER T W	2474	FREED L A	1214
CUTHBERT F J	2401	FRIEND M	2323
DAAN S	1976	FRIEND M	2331
DANCHIN E	1641	FRIEND M	2356
DAUGHERTY C H	525	FURNESS R W	1678
DAVIDSON N C	2228	FURNESS R W	2239
DAVIS L S	1352	FURNESS R W	2241
DENNISON M D	504	GASTON A J	2306
DE LAET J	1436	GEE G F	2403
DERRICKSON S R	2402	GELTER H P	592
DHONDT A A	1417	GENTLE M J	1915
DHONDT A A	1436	GERSTBERGER R	2114
DRENT R	761	GNAM R S	673
DROGE D L	932	GOLDSMITH A R	2063
DUMBELL G S	2513	GOSLOW G E JR	701
DUMBELL G S	2561	GOSLOW G E JR	716
DUNNET G M	1639	GOSLOW G E JR	748
DYER A B	1061	GOSS-CUSTARD J D	2199
EADIE J M	1031	GOTO M	2015
EBIHARA S	2015	GOUDIE R I	811
EDWARDS S V	628	GOWATY P A	932
EENS M	1003	GRANT M	2236
ELLIS D H	2403	GRANT P R	1333

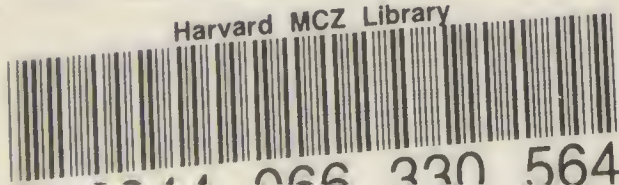
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GRAY R D	2553	JAMES F C	2454
GRIFFIN J M	1273	JAMES F C	2469
GROSCOLAS R	2177	JAMES H F	420
GRUBB T C JR	1432	JÄRVINEN O	1479
GUSTAFSSON L	1425	JENKINS P F	1262
GWINNER E	2005	JENKINS P F	1285
GWINNER E	2022	JIMENEZ J E	1480
HAIG S M	2410	JOHNSON N K	600
HAILA Y	2286	JONES D R	1893
HANDRICH Y	2177	KARASOV W H	2159
HASEGAWA M	2015	KATO A	1393
HASKELL M	860	KEAST A	419
HAUSBERGER M	1262	KEAST A	435
HAY J R	2523	KEMP A C	483
HEINSOHN R G	1309	KEMPENAERS B	1436
HELDMAIER G	2042	KENAGY G J	1976
HENDERSON I M	860	KERLINGER P	1122
HINSLEY S A	1757	KETTERSON E D	1229
HIRTH K-D	722	KIKKAWA J	578
HIXON M A	1156	KIKKAWA J	1195
HOCHACHKA W M	1514	KIKKAWA J	1204
HÖGSTEDT G	1584	KIKKAWA J	1240
HOLMES R T	1542	KING J R	2186
HOLMES R T	1559	KLINKE R	1805
HOMBERGER D	398	KLOMP N I	1678
HORNE J F M	468	KOMDEUR J	1325
HOWE R W	903	KOOYMAN G L	1887
HUGHES M R	2138	KORF H-W	2006
HULSCHER J B	889	KORPIMAKI E	1528
HUMMEL D	701	KREIG M	611
HUMMEL D	730	KRUIJT J	1068
HUMMEL D	748	LAL P	2030
HUNT G L JR	2272	LAMBECK R H D	2208
HUNTER F M	1347	LAMEY T C	1741
HUNTER M L JR	2283	LANK D B	1666
HUSSELL D J T	947	LAWLER W G	843
ILYICHEV V D	91	LAYBOURNE R	2454
IMBER M J	1377	LE MAHO Y	1777
IMBER M J	1402	LE MAHO Y	2177
IMBER M J	1413	LEBRETON J D	2384
INNES J G	2523	LEE S C	1734
IRONS D B	2378	LEE W G	1617
ISENMANN P	2384	LEVEY D J	1624
JACKSON D B	2236	LOUETTE M	475
JACKSON S	1378	LOVVORN J R	1868

LUNDBERG A 1360
LYNCH A 1244
LYON B E 1023
MAJER J D 1568
MANN N I 1074
MARTELLA M B 681
MARTIN G R 1091
MARTIN G R 1130
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MARTIN L F 681
MARTIN T E 1595
MASMAN D 1976
MAURER B A 826
MAURER B A 835
MAY R M 1012
McDONALD M V 1245
McFARLAND D C 1141
McKINNEY F 868
McKINNEY F 876
McKINNEY F 885
McLEAN I G 1273
McNAB B K 860
McNEE S 1166
McNEIL R 1098
MEATHREL C E 2390
MEIRE P M 2219
MELANCON M J 2474
MENCH J A 1905
MERTON D 2514
MIGOT P 2365
MILLENER P R 127
MILLS J A 1522
MILLS J A 2390
MINOT E O 929
MINOT E O 992
MOCK D W 1703
MOCK D W 1741
MOERMOND T C 903
MØLLER A P 1001
MØLLER A P 1041
MONAGHAN P 2257
MONAGHAN P 2365
MONNAT J-Y 1641
MONTEVECCHI W A 2246
MOORE F R 753
MOORE F R 787

MOORE F R 1122
MOORHOUSE R J 690
MUMME R L 1317
MURPHY M E 2186
MURRAY K G 1605
NACHTIGALL W 722
NAGY K A 793
NAITO Y 1393
NAVARRO J L 681
NEE S 1012
NEMESCHKAL H-L 459
NESMITH C 2454
NETTLESHIP D N 87
NETTLESHIP D N 2239
NETTLESHIP D N 2263
NEWTON I 1689
NEWTON I 2487
NEWTON L 860
NOLAN V JR 1229
NORMAN F I 876
OBST B S 793
OBST B S 920
OEHME H 737
OHLENDORF H M 2474
ORING L W 2072
ORMEROD S J 2494
OSHIMA I 2015
OWEN M 1105
PAABO S 554
PAIN D J 2343
PANT K 2030
PARKIN D T 2435
PARKIN D T 2469
PÄRT T 1425
PATON D C 1156
PATON D C 1611
PEARSON D L 1462
PELLATT E J 1347
PERRINS C M 1499
PERRINS C M 1500
PETERS D S 572
PETERSON R W 91
PETRIE M 1001
PETRIE M 1041
PHILIP HRH THE PRINCE 107
PIATT J F 791

PIATT J F	811	SAITOU T	1196
PIATT J F	2272	SAUNDERS D A	653
PIENKOWSKI M W	2228	SAUNDERS D A	658
PIERSMA T	761	SAUNDERS D A	697
PIERSMA T	2228	SCHARF W C	2372
PINXTEN R	1003	SCHODDE R	404
PLACE A R	913	SCHODDE R	413
PLACE A R	1378	SCHODDE R	611
PLUNKETT G	1244	SCHUCHMANN K-L	305
PONGANIS P J	1887	SEMM P	1813
POTTER M A	2092	SHEEDY C	611
POWELL A N	2423	SHERRY T W	1542
POWER D M	545	SHERRY T W	1559
PRATT T K	425	SHORT L L	468
PRICE D K	1367	SIBLEY C G	61
PRINCE P A	1113	SIBLEY C G	109
PRINZINGER R	1755	SIEGFRIED W R	450
PRINZINGER R	1799	SILVERIN B	2081
PRÜTER J	2365	SIMON E	2105
QUINN T W	628	SLAGSVOLD T	1703
QUINN T W	2441	SLAGSVOLD T	1707
QUINN T W	2469	SLATER P J B	1074
RALPH C J	1444	SMITH D G	2403
RAPOPORT E H	826	SMITH J N M	1514
RATTNER B A	2474	SORENSEN L G	851
RAYNER J M V	702	SPAANS A L	2361
REBELO A G	1180	SPAANS A L	2365
RECHER H F	1470	SPAANS A L	2396
RECHER H F	1568	SPURR E B	2534
REED C	2514	STANGEL P W	2442
REINERTSEN R E	1755	STANGEL P W	2469
REINERTSEN R E	1799	STEADMAN D W	424
RICKLEFS R E	929	STEVENS G R	361
RICKLEFS R E	992	STOLESON S H	1727
RIDOUX V	1392	STRIJKSTRA A M	1976
RISEBROUGH R W	2480	STURGES F W	1559
RISING J D	534	SUHONEN J	1418
RISTAU C A	1937	SULLIVAN K A	1957
ROBERTSON H A	1617	SUTHERLAND W J	2199
ROBERTSON R J	974	TEGELSTROM H	592
ROBIN J-P	2177	TEMELES E J	1156
ROCKWELL R F	1666	TEMPLE S A	2298
ROGERS C M	1514	TEN CATE C	1051
ROOT T	817	TEN CATE C	1081
RUSSELL R W	1156	TERRILL S B	751
RUSTERHOLZ K A	903	TERRILL S B	752

THALER E	1791	WIENS J A	1461
THIOLLAY J-M	1489	WIERSMA P	761
THIOLLAY J-M	1576	WILEY J	2417
THOMAS D H	1757	WILLIAMS J B	1964
THOMAS D H	2122	WILLIAMS M J	841
THOMAS N J	2331	WILLIAMS M J	860
THORNHILL R	1361	WILLIAMS M J	876
TIEBOUT H M III	1175	WILLIAMS T D	1393
TIEBOUT H M III	1605	WILLSON M F	1630
TRIGGS S J	525	WILSON A C	554
TRIGGS S J	860	WILSON A C	628
UTTLEY J D	2257	WILSON A C	2441
VAN HORNE B	2313	WILSON J B	1617
VAN DEN ELZEN R	459	WILSON R P	1853
VAN NOORDWIJK A J	2433	WILTSCHKO W	1803
VAN NOORDWIJK A J	2462	WILTSCHKO W	1845
VAN NOORDWIJK A J	2469	WILTSCHO R	1803
VAUK G	2365	WILTSCHO R	1845
VELTMAN C J	860	WINGFIELD J C	2055
VERHEYEN R F	1003	WOBESER G	2325
VERMEER K	2378	WOBESER G	2356
VICKERY J A	2494	WOLF L	1229
VUILLEUMIER F	327	WOOLLER R D	1657
VUILLEUMIER F	354	WOOLLER R D	2390
VUILLEUMIER F	553	WORTHY T H	555
VUILLEUMIER F	578	YAMAGISHI S	1195
VUILLEUMIER F	587	YAMAGISHI S	1220
WALLACE M P	2417	YAMAGISHI S	1240
WATTS C	1012	YOUNG B E	1605
WEATHERS W W	1957	YUILL T M	2338
WEBSTER M D	1765	ZACK S	1301
WENZEL B M	1820	ZIEGENFUS C	1229
WETTON J H	2435	ZINK R M	591
WHITEHEAD M D	1384	ZINK R M	629
WHITELEY P L	2338	ZWEERS G A	897



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